

THE POTENTIAL OF *ARIZONA CAME* (LEPIDOPTERA: NOCTUIDAE)  
FOR THE CONTROL OF MARIJUANA WITH SPECIAL  
REFERENCE TO THE ECOLOGY OF MARIJUANA  
(*CANNABIS SATIVA*) (WALT.) SAMPSON

By  
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A DISSERTATION PRESENTED TO THE  
GRADUATE COUNCIL OF THE UNIVERSITY OF FLORIDA  
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS  
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY  
UNIVERSITY OF FLORIDA  
1964

## ACKNOWLEDGEMENTS

I wish to thank the numerous individuals who have assisted in these studies.

I would like to express my appreciation Dr. E. C. Griswold, Dr. E. C. Todd, Dr. H. E. Veenhoff, Dr. T. J. Walker, Dr. S. Carlson, and Dr. C. R. Sidersky for the identification of insect specimens; Dr. G. E. Piles, L. P. Rish, and Dr. E. L. Howard for diagnosing insect diseases; C. Capin, E. Sidersky, M. White, R. Freaser, S. S. Spencer, and B. Butler for field and technical help; the University of Florida Insect Laboratory for analyzing water samples; Dr. E. A. Barker for providing solar radiation data; the U. S. Department of Agriculture and the Florida Division of Plant Industries for providing space and facilities; Ann Beets and Susan Green for library and literature research assistance; Beth Sidersky for typing and editorial assistance in the original manuscript; R. S. Spencer and T. L. Carlisle for photographs and dark room assistance, and my graduate colleagues, Dr. G. R. Hackett, Dr. T. E. Walker, Dr. H. L. Butler, Dr. S. C. Allen, and Dr. J. McIsaac for critical reading of the manuscript.

I would especially like to thank Mr. Earl S. Spencer for providing space and facilities and the U. S. Army Corps of Engineers for providing funds.

I would also like to thank my wife, Debbie, whose patience and endurance saw me through to the completion of this work.

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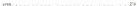


















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Abstract of Dissertation Presented to the  
Graduate Council of the University of Florida in Partial  
Fulfillment of the Requirements for the Degree of Doctor of Philosophy

THE POTENTIAL OF JUVENILE MOSQUITOES FOR THE CONTROL OF  
MALARIA WITH SPECIAL REFERENCE TO THE  
CONTROL OF MALARIA IN THE FLORIDA COASTAL PLAINS

By

Paul Douglas Center

June 1978

Chairman: Dr. John E. Hubert  
Paper Department: Entomology

*Anopheles albopictus* (Skuse) (Diptera: Culicidae) is one of the world's most aquatic mosquitoes. Many countries have begun to consider biological control as a means to eliminate malaria. The United States has begun introductions of exotic insects for this purpose. To evaluate properly the success or failure of these introduced insects, background information on the ecology of *Anopheles albopictus*, the effects of insect attack on *Anopheles albopictus*, and the population biology of both system insects in the area of release is imperative. The purpose of this dissertation is to provide this information for Lake Wales, a primary study site at the University of Florida campus.

The ecology of *Anopheles albopictus* is approached in this dissertation through a comprehensive literature review and through field studies conducted to monitor various growth parameters. Sexual productivity

corres comparing small and large plants revealed that the net efficiency of both plants was 1.6% (of incident solar energy); the small plants grow faster than the large ones, however, in virtue of a larger F/R ratio (2.06 vs. 1.66).

Photosynthetic efficiency is maintained by specialization of the leaf area index with the incident solar energy flux. An annual increase in leaf area occurs first through an increase in leaf density and secondly through an increase in leaf (ground)lengths. The net result of these two growth phases is a peak in the leaf area index spanning the period of maximum solar radiation.

Intraspecific competition is strongly indicated in governing plant density and seems to account for observed changes in the population. Plant density is high in the winter reaching a maximum in April. This is followed by a decline in May and June as a result of the loss of plants in the smaller size classes. This loss is due to shading by the larger plants as they increase in size and leaf area.

Multivariate analysis indicates that solar radiation and stream air temperatures were important in accounting for changes in standing crop, plant height, leaf area index, and the number of leaves per plant (all indices of biomass). The introduction of water quality parameters into the analysis resulted in confusion as causal relationships were difficult to establish.

Damage by crown dove *Myiophobus* (family *Columbidae*) did not appear to affect the population of waterhyacinth studied. Quantitative studies revealed that consumption of 25 leaves per 100 plants would significantly reduce almost all characteristics examined and greatly accelerate

latter? A seasonal aspect was implicated in the plant response as the insects appeared to be much more effective in the fall than the summer. This may be related to the energy budget of the plants under varying conditions of solar flux. Plant density increased in the summer in response to insect attack, probably as a result of decreased intraspecific competition. A similar response would be expected in dry flaxen which without competition provided adequate energy for growth was available.

To learn if *A. absona* could be used in biological control a green-house control population was released on a small pond in August 1976. The waterhyacinth population was reduced and competing plants began to dominate the site. Eventually wet-land lilypond and waterhyacinth failed to re-form. A control site remained dominated by waterhyacinth.

Studies of natural *A. absona* populations on Lake Allen indicated that the failure of this insect to achieve sufficient levels to have an extensive effect on waterhyacinth was most likely due to the complex of parasites which attack them. Also, pickerelweed (*Sparganium angustifolium*) appears to be the preferred host of this insect which may partly explain the low population observed on waterhyacinth. Further, seasonal changes in the plants' ability to withstand insect attack may obscure correlation between plant characteristics and insect damage.



## INTRODUCTION

At the start of this study various state and federal agencies were preparing for the release of weevil insects for the biological control of waterhyacinth (*Eichhornia crassipes* (Thunb.) Solms) in Florida and the Caribbean I L. In order to evaluate the effect of these insects it was apparent that prior information on the ecology of waterhyacinth at the release sites, particularly with regard to annual variability, and the effects of indigenous insects would be needed. The purpose of this dissertation was to provide part of this information for Lake Alice, the primary study site in the Suwannee area.

To achieve this end the annual sequence of events in the waterhyacinth population was studied as well as the actual and potential effects of natural and introduced predators of *Aeneides* *Aeneides* spp., a native insect which feeds on waterhyacinth. This dissertation is organized into five sections. The first section is a literature review organized into two parts. The first part reviews the biology of waterhyacinth and is organized in a manner similar to that reported by Green and Mulligan (1977). The second part reviews the taxonomy and biology of *A. Aeneides* spp. and related species.

The second section is a study of the waterhyacinth population on Lake Alice. A fairly detailed description of the study site is provided. The phenology of various morphometric features of the waterhyacinth population is described with regard to the possible influence of various physical and biological factors. A short study on the productivity of waterhyacinth is also included in this section.

The third section investigates the potential effects of *A. jamaicensis* on greenhouse cultures of waterhyacinth. These effects are evaluated in terms of various ecological and morphological traits of the plant.

The fourth section deals with the feasibility of augmenting natural populations of *A. jamaicensis* as a means of biological control. The effects of a small scale release are evaluated from a small pond near Payson, Arizona.

This fifth section constitutes notes on the biology and life history of *A. jamaicensis*. Data on the natural population at Lake Elton is presented and the probable reasons for the failure of this insect to control waterhyacinth is discussed.

It is hoped that the information reported here will provide a baseline from which future comparisons can be drawn after the release of exotic insects. It is also hoped that an increased understanding of the ecology of waterhyacinth in a situation relatively free of specific insect enemies has been gained.

## LITERATURE REVIEW

### *Eleocharis acuticarpa* (Pers.) Solms.

#### Summary

Beck (1944) provides an excellent historical review of the Thais where dealing with the taxonomy of *Eleocharis acuticarpa*. The most current treatment of the genus appears to be that of Hitchcock (1944) which describes the species occurring in America. Five species are described (*E. acutis*, *E. acuticarpa*, *E. densiflorus*, *E. heterocarpa*, and *E. parviflora*) and a key provided. The synonymy provided for *E. acuticarpa* is as follows:

*Eleocharis acuticarpa* (Pers.) Solms. in DC., *Monogr. Phan.* 4: 317 1845  
*Eleocharis acuticarpa* Pers., *Mon. Gen.* 1: 8 1, 4, 1806  
*Eleocharis acuticarpa* (Pers.) Raf., *Fl.* Ind. 2: 88, 1823.  
*Eleocharis acuticarpa* (Pers.) Donn., *Fl.* 4: 121 1825  
*Eleocharis densiflora* (Pers.) Hitchc., *Proc. Bot. France* 84: 274 1927

While the historical *E. acuticarpa* is in common usage today the synonym *Eleocharis acuticarpa* and *E. acutis* are common in the literature.

Because of the world-wide distribution of this plant it is known by a large variety of common names. Beck (1944) lists 46 common names for *Eleocharis acuticarpa* from 18 countries. The name waterhyacinth is used world-wide in scientific reports but the structure of the word has often been left up to the discretion of the user. It is often written as two words (water hyacinth), a hyphenated word (water-hyacinth), or as one word. Kelsey and Sargent (1942) in a list of standardized plant names use the single word, waterhyacinth. This usage seems appropriate since the plant has related to hyacinth as the two word name would

help. For this reason I follow Selous and Burton (1861) and use the spelling *stictopygus* throughout this description.

Suborderlele is a member of the pichardsoni family which includes 8 genera and 36 species (Cook et al. 1979). The genera are *Psiloborus* (1 spp.), *Myrmecops* (1 sp.), *Neomethys* (10 spp.), *Epithorax* (1 sp.), *Monochorus* (6 spp.), *Pontodorus* (9 spp.), *Amazilia* (4 spp.), *Stictopygus* (1 sp.), and *Isotrochus* (1 spp.). The majority of the members of this family are confined to the Americas although two of the genera (*Monochorus* and *Stictopygus*) appear to be Old World endemics. Keys and descriptions of the genera (worldwide) may be found in Cook et al. (1979). Lewin (1973) revised the genus *Pontodorus* and added *Amazilia* with 11. Castellanos (1988) provides notes on the genus *Pontodorus* in Brazil and keys and descriptions of the Brazilian species of *Pontodurinae* (Castellanos 1988).

### Identification and Account of Variation

Following is a translation of the description of *Psiloborus erasmii* (Bart.) taken directly from Selous (1874). Further descriptions can be found in Castellanos (1988), Smithers (1967), Beck (1966), Posthum and Darb (1963), Bucken and Co. (1936), Moore (1937), and many others. The first definite description of this species (according to Beck 1966) was that of Smith (1843).

Plants floating or sometimes fixed to the substrate, the leaves in the form of a rosette with the stem reduced and the plants connected by an elongated horizontally ridged, anastomosing rhizome arising from each plant. The aerial leaves are variable in shape, petioles of 1 to 30 cm long are more or less inflated, elliptical 2-15 cm long with a small apical reticulate-veniform lobe with a lobulate (aurate?) margin, submarginal leaves never evident. Inflorescence variable, inflorescence between the apices nearly absent. Inflorescence with leaves 1-4 cm long, the sheath 2.5-7 cm long. Flowers 4-6 cm long, perianth light purple or nearly white, tube 1-1.5 cm long, lobes 2.5-4.5 cm long, with entire margins. Stamens 10-12, stamens villous-glandular. Capsule ellipsoid, trigonous, 10-15 cm long, seeds oblong-ellipsoid 1.5-2.5 x 0.5-0.8 cm with 10 longitudinal ridges. Observed 1934, 1950.

The leaves of waterhyacinth are variable in the shape of the blade and the extent of development of the float. This variability is apparently due to the plant response to environmental conditions. It was shown prior to 1930 that the size of the floats depends on such factors as light, temperature, and water quality (Le Gendre 1930). Rao (1936a) has concluded that increased water uptake (in a hydrostatic method) promoted the development of the float. This is discussed further by Rao (1936), Pandey and Veria (1944), and is an exceptionally good account by Hiron (1955).

The waterhyacinth flowers are possibly trimorphic with regard to the length of the style. Although short and long styled forms are known, the existence of short styled forms is thought to be possible (Rao 1936). The obdiplostemon form is normally predominant and Rao (1936) holds that only the old and long styled forms exist. The flowers possess two whorls of anthers which Rao (1936) notes are long and short in the old-styled form and short and old-length in the long-styled form. This description is apparently regulated by a fan gene system, the starting anther

effect on the river, and such goes with the siltation [Beck 1988; Groot 1988]

Very few cytological studies have been done on waterhyacinth. Koenigs (1974) found the chromosome number to be  $2n = 28$  in leaf, illustrated karyotypes, and described the chromosomes. She found the chromosome number to be very consistent but noted variations of  $2n = 22$  and  $4n$ . Beck (1988) also reported the diploid chromosome number to be  $2n$  and noted that this had been reported by earlier authors as the probable number.

### Ecological Importance

Waterhyacinth is ranked world-wide as among the top 10 most important weeds and as the single most important aquatic weed [Bello 1989]. Because of its floating habit and high productivity [Beck 1988] it competes with man for open water. Large build-ups interfere with hydroelectric operations in many areas [Bello, et al. 1989; Bunting 1984]. Its ability to interfere with navigation is well documented [Ray 1989; Owen 1982, Bello 1988, Kumar 1982, Curtis 1980, Zenger 1982]. In the Amazon basin mats of waterhyacinth have become so thick as to interfere with the opening and closing of the locks [Hazen, pers. comm.]. Bello, et al. (1989) cited a study in which the efficiency of canals in the Amazonian were reduced 40-60% by large infestations of this plant. Irrigation operations are affected by the impoundment of water flow and the clogging of pumps.

Waterhyacinth affects agriculture not only indirectly, as in irrigation, but also directly - sugar and rice are cultivated in "float-fallow"

irrigation where the field is flooded for several weeks. Aquatic weeds compete with the crops for the open surface, increase evaporation, and may provide reservoirs of crop pathogens (Nat. Sci. Soc. Trans. of Egypt and S.A.S., 1953).

Water losses through evapotranspiration by waterhyacinths can be considerable. Thomas (1968) showed that 17 states lose nearly 2 million acre-feet of irrigation water annually due to aquatic and ditch bank weeds. Hahn *et al.* (1955) quoted an estimated value of this lost water as over 120 million. Rates of evapotranspiration by waterhyacinths are reported by Redmond and Earle (1941), Thomas and Nelson (1967), Weiss (1961), Brown *et al.* (1973), and Van der Meert and Busseling (1974). These reports conflict, however, as experimental techniques appear to be a large source of error in these studies. The ranges of the ratio of transpiration to open water evaporation are 1.68-4.4 (Redmond and Earle 1941), 3.7 (Thomas and Nelson 1967), 1.75-3.24 (Weiss 1961), 1.08-1.28 (Brown *et al.* 1973), and 1.28-1.54 (Van der Meert and Busseling 1974).

Large mats of waterhyacinths covering the surface of water bodies block light to phytoplankton and submersed vegetation. This effectively prevents the translocation of oxygen through the photosynthetic processes of these organisms. Further, surface diffusion of oxygen is lowered to a degree as high as 70% at the air-water interface. This results in a severe reduction of dissolved oxygen (Otis 1971). This renders the habitat unsuitable or lethal to many desirable species of fish. Adams and Boyd (1975) demonstrated that extensive pond coverings by waterhyacinths reduce phytoplankton growth and fish production. The competition of

the aquatic food chain may change from a plant-herbivore based community to a detritus-detritivore based community [e.g., Meade et al. 1983] as a result of this loss of submersed primary productivity.

Eutrophication may also successfully compete with valuable wildlife forage thereby replacing it. This may destroy feeding areas for waterfowl [Sawaluck 1988]. Local economies may be seriously damaged in areas which cater to recreational needs such as waterfowl hunting, fishing, boating, water skiing, swimming, etc.

More seriously, eutrophic communities in the developing areas of the world which depend on fishing as a primary source of protein may be denied access to fishing grounds [Bain 1985]. Bain [1985] further noted that "improvements for fish culturing may be destroyed by large masses of floating waterhyacinths. He stated that waterhyacinths can "offset" the most serious, most serious and frightening food problem" he had ever known.

Waterhyacinth provides poor a habitat for many vectors and intermediate hosts of human diseases. The brown red pupae of *Anopheles stephensi* [Thoms ], a mosquito vector of *Plasmodium* m. sp., are known to attach to the roots of waterhyacinths [Burton 1988, Kocumova 1989]. Waterhyacinths may result in an increased production of mosquitoes by providing insecticide application, interfering with predators, increasing the habitat available for certain species which attach to the plant, and by trapping runoff and water circulation thereby creating stagnant environments for breeding [Sawaluck 1988]. McInneson [1982] contends that uncontrolled aquatic plant proliferation could lead to an increased incidence of mosquito-borne diseases such as malaria, dengue fever, and



other sedentary plants (1990) indicated that aquatic plants, including waterhyacinths, may also harbor snails which are intermediate hosts of diseases such as fascioliasis and streptocytosis. He mentioned that these species which do occur on waterhyacinths are assisted in their dispersal by the free-floating habit of this plant thereby spreading the associated diseases. Beck (1988) further reviews the literature dealing with health hazards caused by waterhyacinths.

It is difficult to arrive at exact figures regarding the monetary losses caused by waterhyacinths. Spencer (1973, 1974) quoted the following figures from a comprehensive report for losses presented by waterhyacinth control in Louisiana in 1967:

Navigation	\$ 1,875,000
Flood Control	unknown
Recreation	1,581,000
Aquaculture	15,567,000
Fish & Wildlife	18,797,000
Public Health	750,000
	\$27,569,000

Parham and Carls (1944) conservatively estimated that waterhyacinths were responsible for losses of \$5 million annually as of 1940 in Louisiana. Spencer (1973, 1974) quoted figures from a Louisiana Fisheries and Wildlife report indicating losses of \$45-75 million in 1967 in Louisiana due to aquatic weeds. In 1960 a report to the Jacksonville City Commission estimated that in the period from 1950-1959 the Federal Government spent \$215,000 on waterhyacinth removal in the Jacksonville District to help maintain "open channels for navigation" (Buchanan and Co. 1964). By 1961 the total cost had risen to \$1,881,700 in the same district (Faulstich and Woods 1964). Huesterlich (1964) reported costs of clearing aquatic weeds ranging from \$15-25 per acre. As of 1965 about

85,000 of Florida's 2,500,000 acres of fresh water and 75,000 to 100,000 acres of Louisiana's 2,000,000 acres of fresh water are infested with waterhyacinth (Jageroff 1974). Nelson (pers. comm.) estimates that in 1975 the acreage of waterhyacinth in Florida has increased to more than 200,000 acres and the average cost of control per acre is about \$25. He estimated that all agencies within the state in FY 1976 allocated \$10 million for aquatic weed control, about 20% of which (\$4.2 million) goes towards waterhyacinth control. This is an increase of almost \$2 million over the previous year (FY 1975) for waterhyacinth control alone.

Thompson (pers. comm.) indicated that between 1965 and 1974 the U.S. Army Corps of Engineers spent \$4.1 million in combined construction and operations funds for aquatic weed control in Louisiana alone. In the period between 1962 and 1964 the estimated cost was \$1.7 million. Boat weeds are of minor concern and for the most part 100% of this went toward waterhyacinth and alligator weed control. The State of Louisiana beginning its program in the mid 1940's spent \$1.1 million in FY 1973. Further costs included \$1.1 million in 1974 and \$1.1 million in 1975. Thompson further estimated that the average cost of treating an acre is between \$32 and \$35 in Louisiana. The most economical means being by helicopter (\$12/acre) or float strip harvesters (\$18/acre) when possible. The current estimate of acreage covered in Louisiana exceeds 1 million acres. This does not necessarily reflect an increase in acreage over Jageroff's (1974) figure but is merely a more accurate estimate.

It is evident from these figures that the acreage covered with the plant is increasing while the cost of treating an acre is also

increasing. The result of this is a progressively increasing threat to the overall state of aquatic and control by traditional means.

Success of the vermiculture of waterhyacinth infestations, the beneficial aspects of this plant have been largely overlooked or ignored. Pragas of aquatic plants along rivers or lakes are often helpful in clearing silt and weed action and preventing bank erosion (Tilgner 1963). Caldwell (1942) notes that the roots of waterhyacinth provide excellent cover for juvenile species. He promotes the growing of this plant for ornamental purposes stating that it is the "biggest bargain in a pond plant . . ." and discusses its detrimental distribution as an " . . . attractive nuisance." Waterhyacinth was originally imported into this country for use as an ornamental (Haynes 1964) and the beautiful flower does give it a certain aesthetic appeal.

Tilgner (1962, 1963) spent many years fishing the St. Johns River and guiding fishing boaters. He was extremely aware of the beneficial effects of waterhyacinth on fish propagation noting that the plant roots provide cover for eggs and support macro-invertebrates which are grazed upon by fish. Tilgner also noted that the plants helped clean the water thus improving the fish habitat.

Spethardt and Pomeroy (1979) studied the influence of waterhyacinth on planktonic development in the White Nile. They compared plankton populations and water chemistry parameters at a site south of Juba Juba dam in Sudan shortly after 1960 before invasion of the area by waterhyacinth occurred. They found that overall planktonic densities had increased in the interior as a result of changes in the water quality (such as an increase in phosphates). They attributed

this change to the weed infestation has failed to consider cultural changes in the area. They concluded that the weed growth provides improved conditions for electrofishing development and thus benefits fish production. The basis for these conclusions is obscure, however, and doesn't agree with the findings of other authors (e.g. Whitfield 1988). Peters and Boyd (1979), while it seems probable that a fringe of the weed would be beneficial in some areas (see (1984) comment "... the various reports of fish mortalities in adjacent ponds and ponds covered with waterhyacinth at once disprove the ideas and rule the proposal that waterhyacinth should ever be planted in tropical countries as 'one of the wonder plants' for any kind of pisciculture."

Increasing attention has been directed towards using waterhyacinth. Fink (1940) advocated utilizing waterhyacinth as a weed. Waterhyacinths are currently being considered for tertiary treatment of sewage effluent (see Spence 1945, McCarthy 1947, Reed 1964, Tsai and Chouhan 1978, Boyd 1979a, Rogers 1979, Rogers and Davis 1981, Santiago et al. 1979, Santiago and Packer 1979). Its possible use as food for livestock (Chatterjee and Roy 1958, Saldaña et al. 1979, Rogers et al. 1979, 1984, Saldaña 1979, Boyd 1979a, El-Saied 1979, Rogers 1979, and Saldaña 1981). Apparently waterhyacinth is used as pig fodder in Singapore (Anonimus 1981). A complete cycle is developed when waterhyacinth is fed to pigs, manure and fecal matter are washed from the pigpen into the pond, this fertilizes the pond to produce fish and more waterhyacinth which are then harvested.

Chatterjee and Roy (1958) found that waterhyacinth can hold 10 pounds with as much as 68% in the root (28 on dry weight), comparable

with other fodders is nitrogen content (0.82 to 2.95 g/kg), rich in chlorophyll (0-10 g/kg), and richer than Barler and Guinea grass in fiber (0.50 g/kg) and lignin (0.002 g/kg). They also noted that its phosphate content was low (0.001 g/kg) but that the digestible nutrients compared well with other fodders. Taylor and Roberts (1961) analysed the composition of waterhyacinth and found the leaves to contain 16.00 dry matter which in turn was composed of 14.70 ash, 1.70 nitrogen, 10.70 crude protein and 170 crude fiber. The whole plants were 8.00 dry matter, 1.00 nitrogen and 0.00 crude protein. They also analysed the plants for the amino acid composition. They concluded that the lysine content of waterhyacinth was sufficient to serve as an effective amino protein supplement.

Boyd (1964) determined that waterhyacinth contained 10-100 (g/kg) crude protein. He subsequently fully analysed the nutritive value of waterhyacinth and found the dry weight to be 5.00, the crude protein to be 0.002 of the fresh weight (0-100 g/kg), cellulose 0-100 (g/kg) total available carbohydrate 7.00, ash 170, and caloric content ca. 3.0 kcal/g. He further analysed the inorganic nutrient content and the amino acid composition. Taylor et al. (1961) extracted proteins from waterhyacinth and found that the percentage on a dry weight basis varied between 3-4 to 10-15. They also analysed the proteins for the amino acid composition.

Rajaling et al. (1966) compared the nutrient content of waterhyacinth from two different sites. They performed comparative analysis of various plant parts from the two sites for nitrogen, phosphorus, calcium, potassium, and magnesium as well as chlorophyll and water

content. They determined that the nutrient content in the plant tissues was not dissimilar to that of the water in which they were grown. Boyd [1974] has summarized the data on the composition of waterhyacinth and other aquatic plants.

Cheng and Lovell [1971] evaluated waterhyacinth for use as channel catfish feed. They found that the addition of 5 to 10% waterhyacinth to vitamin free diets increased growth and reduced mortality in the fingerlings.

Bagall et al. [1970] using waterhyacinth as feed supplements for cattle and sheep, for paper production, and for which determined that the processing as such was the most economically feasible use.

Khan [1961] proposed that underdeveloped countries encourage their people to utilize their spare time preparing various products made from waterhyacinth and thus supplement their income. Some of the products they suggested were paper, printed board and tiles, artpapers, office folders, and more. Raju and Kirese [1970] considered waterhyacinth suitable in the production of paper.

Isaacs and Ben [1971] found that an extract from waterhyacinth roots increased the yield of fringed (*Chlorella vulgaris* var. *fringed*) from 50.2 g/ha to 107.2 g/ha. Garguly and Simon [1969] found that a root extract from waterhyacinth increased the metabolic activity and the nitrogen and sugar content of *Alnus incana* L. seedlings. Bhattachar et al. [1966] identified growth promoting substances in the roots of waterhyacinth which they believed to be steroid nuclei. Gurlik et al. [1964] noted that this extract was thermostable and found it to promote the growth of *Stenococcus mageritae* *melanophilus*, the mycelium of *Aspergillus niger*, the growth of *Stenopus*, and the multiplication of

yeast cells thereby providing fermentation. S.B. Jirassri and Chakravarty (1980) found that this yeast extract increased the yield of *Yersinia enterocolitica* L.) and the production of fiber. R.B. Miran et al. (1979) isolated four glycerol-116 compounds from extracts of *Leishmania* *donovani*.

Other attempts to find valuable products of *Leishmania* include ink, apothecary stuffing, soap, soap, plastics, linker substitution, and the chitin (Duck 1944). Huxley (1981) gives a recipe for preparing *Leishmania* for food. For further review of the literature dealing with the utilization of *Leishmania* and other aquatic insects see Duck (1944), Southwark (1967), Little (1966), Fox (1972, 1975) and Huxley (1981).

### Distribution

It is generally accepted that South America is the area of origin of the *Leishmania*. Duck (1944) indicated that it was originally discovered in the San Francisco River near Manaus, Brazil in 1904. Duck (1944) cites Huxley (1929) as listing several early collections from Brazil, Amazon River, Guiana, Rio Grande (a former Spanish colony including present day Venezuela, Ecuador, Colombia, and Panama), Guyana, Ecuador, and Buenos Aires, Argentina. The first other early references indicating it was also native to the West Indies (see Schwartz 1926, Britton 1933). Castellanos (1946) lists its present South American distribution as Argentina, Paraguay, Brazil, Uruguay, Chile, Ecuador, Colombia, and Guyana. It has also been reported to Surinam (Little 1966, 1968, Fox et al. 1973). It has apparently been widespread in South America for many years as evidenced by the early records.

Wiese (1988) cited a source which indicates that the center of origin for this species was probably the Kanto region of Japan. A few authors have subscribed to other regions of origin within of South America. Hildebrand (1961, p. 477) states "The water hyacinth, *Eichhornia crassipes*, is a native of Japan and was carried about 70 years ago to South America, where it became widespread in fresh-water streams and lakes." He cites Swasey (1944) as the authority for this statement. Swasey apparently contradicts himself, however: in one paragraph he does indicate that waterhyacinth is native to Japan and was imported to South America. In the following paragraph he states, "When in 1884 an International Cotton Exposition was held in New Orleans, the Japanese Government representatives in their building on the Exposition grounds gave away to numerous water hyacinths which they had imported from Yamanashi." Swale (1988) suggested that it may be native to Florida. A Japanese author claimed that Florida was its area of origin (Buck 1983).

Waterhyacinth is well known from the West Indies (Buck 1983). Castellanos (1985) included the Antilles within the range of distribution. Ramirez (1985) also indicated that the plant was present in the West Indies--Buck (1983) cited a paper which indicates that Puerto Rico is the center of dispersal for this species. The plant found in Guatemala is Jamaica. She suggests that it may have spread to the islands attached to Haiti or by floating from the mainland.

As might be expected waterhyacinth is also known from most of the Central American countries including Panama (Muefling 1978, Hearn 1980), Costa Rica (Little 1988), Nicaragua (Little 1988, 1989, Hearn et al. 1988), Honduras (Castellanos 1985), and El Salvador (Little 1988, 1989, Hearn et al.



1940). I have not found any records of waterhyacinth occurring in Guatemala but its range does extend into Mexico (Castellanos 1958, Little 1994) where it is apparently well distributed.

As previously mentioned waterhyacinth was thought to have been introduced into the United States from Guatemala in 1884 at the International Cotton Exhibition in New Orleans by the Japanese delegation (Clarer 1908, Burden and Co. 1928, Spearlock 1940, Wilschke 1944, Spear 1948, Postland and Earle 1949, Takita and Smith 1949, Sutton 1964, Wilschke 1964, Koch 1964). Some accounts indicate, however, that the plant may have been in the United States in the 1840's (Takita and Smith 1949) or prior to the Civil War (Postland and Earle 1949). The accepted theory maintains that the plant was given away as souvenirs at the New Orleans Cotton Exposition (Spearlock 1940). The plants were taken for ornamental purposes (Clarer 1908, Sutton 1964, Wilschke 1964) or for purposes of utilizing them for cattle fodder (Wilschke 1964). In any case, it was felt that when the plants reached the United States of Spain given them they were sent out into natural bodies of water (Clarer 1908). By 1888 it was in the coastal fresh waters of Texas, Louisiana, Mississippi, and Alabama (Burden and Co. 1928).

It was apparently introduced into Florida in 1890 (Miller 1947, Adams 1951, Barber and Rogers 1959, La Gade 1960, Burden and Co. 1928, Postland and Earle 1949). Rogers (1944) reported it was first introduced to the St. Johns River at Apopka about 4 miles above Tampa. Dr. J. J. Lucas was interviewed by a New York Times reporter (Anonymous 1964) in 1964 and gave the following account:

"I have the man who brought the first plant to Florida," Dr. Lucas

used to a bus reporter, "and he thought that he did the State & Fair! I have it from his own lips, and I've known him since long before that time, for I used to carry him up the river in a launch year after year to his orange grove. He was Mr. Fuller, father of A. F. Fuller of Weekiwahe, owner of Siquemaw Grove, a property which he thought not improved, until now it is a beautiful place, seven miles above Fortlake. Five years ago there wasn't a water hyacinth in the St. John's River, nor in the state, so far as I know. Now because Mr. Fuller brought some there and put them in a pond on his premises. I understood that he brought them from Europe. They added very much to the beauty of the place, and they decided so that he took some and threw them into the river. There they grew and blossomed abundantly, and they were greatly admired, and Mr. Fuller said to me one day "The people of Florida ought to thank me for getting these plants here."

"But presently there is this pond and spread so that they covered it over. Then he cleared them off and--but it was too late to stop them from spreading all over the river. They worked their way and were blown up and down the river, and into the bayous, and finally up the Suwannee [sic]. Two years ago they had become a serious menace to navigation, and protest after protest was sent to the Government. At last the War Department sent an agent to investigate, but he got to us just after the destruction of that heavy frost of two years ago, which killed all our orange trees. The hyacinths were killed too, apparently, and so the agent reported that nature had cleared the river and that there was nothing requiring the department's attention. But the plants were only

dead at the top. They grew again, and the startling condition that you see in these pictures are a growth of only two years."

This account surprisingly indicates that the plants were introduced into Florida from Europe rather than from Louisiana as has generally been assumed (Quackenbush and Co. 1938; Tarrill and Weeks 1944; Westerlich 1944).

*Wisteria* was first discovered in Memphis in 1900 (Harner 1940) about one mile north of Jackson. The first record in California is from 1904 near Clarkburg, Tulo Co. (Week 1944). Johnson (1938) reported it in Fresno Co., California; Week (1944) lists its present range in California from 10 mi. SE Sacramento (on 36-37° N lat.) (in Butte, San Diego Co. (on 32-33° N lat.); She speculates that it was probably brought to California as an ornamental and released. The primary rivers inhabited are in Central California and include the Kings, Tule, San Joaquin, and Sacramento River Systems.

The introduction of *wisteria* to California is associated with the North American range of this weed. Pearson and Davis (1940) stated that shortly after the turn of the century it had been reported from all the southeastern coastal states as far north as Virginia. A distribution map published by the A.S.G.A. (1936) indicates that the present range of this plant in the U.S. includes the Potomac River in Maryland-Virginia, west to southern Missouri, north to eastern Texas and southern Florida, and westerly, central California.

Just when *wisteria* spread to the Old World is not certain. Spearl (1936) indicated it may have been introduced into India around 1780. Wilson (1932) cited testimony indicating that it may have been present in Bengal as early as 1798 or 1801. It was apparently introduced

to the Gallinuley Solenota Serpentes in Java in 1814 (Buck 1944, Scott-Shorton 1962). By 1828 it had appeared in Ceylon (Japson 1833). It had become a serious problem in Dutch China (a part of S. Vietnam) by 1838, in Java by 1811 and in Bengal by 1814 (McLean 1922). The Portuguese considered the plant around 1652 and by 1828 it was spreading in China as well as Borneo and Malaya (Buck 1944). Records as to its entry to Japan are scarce but they were apparently introduced during this century as ornamentals (Sakabe et al., 1966, Buck 1944). The first record of its occurrence in Okinawa was in 1862 (Buck 1944) but it may have been there earlier.

From Dutch East-Indies it now occurs throughout India, Southeast Asia, and Indonesia (Kamrath 1913, Barber and Heyne 1929, Japson 1833, Pearson and Davis 1938, Anonymous 1934, Sen 1945, Little 1960, 1966, Bala et al. 1969, Chatterjee and Singh 1970, Singh 1960, Hitchcock et al. 1949, Nelson 1932, Agarwal 1974, Robertson and Thiele 1928, Wehner et al. 1965, Sampson et al. 1957, Ishikawa 1962)...

*Metarhizium* was first introduced into Australia or Queensland in 1915 (McLean 1922) and to New South Wales in 1918 (Baker et al. 1924). It was apparently eradicated from New South Wales but a reinfestation occurred in the 1940's (Parsons 1948, Pitt 1949). In South Australia by 1927 (Pitt 1949) and in Victoria by 1928 (Parsons 1948). Pitt (1949) notes that *metarhizium* is not a serious problem in Australia today except in some Queensland rivers.

*Metarhizium* also occurs in New Zealand (Jalilar 1949, Taylor 1959, Anonymous 1944a, Little 1969, 1944a, Bala et al. 1969) although it is difficult to determine when it first appeared there. Taylor (1959)

seems to imply that it was discovered in 1948 at least on the National District. Bellier (1954) reported it from the opposite side of North Island near Dunedin. Matthews (1962) stated that there were 2 acres of infestation in 1948-50, 11 after 1950, and 70 by 1960. Another report (Anonymous 1961) indicated that there were at least 40 acres infested in New Zealand ranging from Otago in the north to Dunedin in the south. Kerton and Kerton (1963) noted its occurrence as far north as Rotorua.

The spread of this plant has also taken to some of the Pacific Islands. It was reported from Hawaii in 1946 (Rock 1946) and Rose and Barlow (1964) indicated that it was recognized as a pest in Fiji.

In Africa the plant is known from Kenya (Anonymous 1962), Zaire (Anonymous 1967, Labrous 1968, Kirkpatrick 1968, Coats 1974, Borg 1976, Little 1980, 1983a,b,c,d,e,f,g,h,i,j,k,l,m,n,o,p,q,r,s,t,u,v,w,x,y,z, 1985), Tanzania (Anonymous 1962, Little 1980), Uganda (Anonymous 1962), Angola (Labrous 1968, Woodcock 1968), French Guiana in Africa (Labrous 1968), Rhodesia (Labrous 1968, Little 1968, Bole et al. 1969), Botswana (Labrous 1968), Mozambique (Labrous 1968, Rousselle 1968), South Africa (Balfout 1969, Fourcade and Lerin 1969, Labrous 1968, Bole et al. 1971), Madagascar (Labrous 1968), Gabon (Gay 1960, 1962, Barthe 1968, Pottier 1964, Little 1965, 1966, Michel Chabbert and Boute 1966, Bole et al. 1969, de-Weert and Fourc 1974, Gay et Boute and Chabbert 1975, Rousselle and Boute 1975), Senegal (Anonymous 1968, Little 1965, Bole et al. 1969) and Egypt (Little 1965, Bole et al. 1969).

Waterhyacinth was first introduced into Africa either to South Africa or Egypt. Southey (1967) cited a work on Egyptian flora which indicated that it made its appearance in Egypt in the period between

1875-1882 Beck (1944), however, indicated that it was not introduced into Egypt until 1918. It was introduced into South Africa around 1910 as an ornamental and by 1928 was reported from rivers in the Cape Peninsula, George, Geyser, Albany, Port Elizabeth, Uitenhage, Victoria East, and Natal (Gieloff 1938). It had apparently reached South America prior to 1927 as Europeans settling there reported its presence at that time (Giles et al. 1944, Beck 1944).

By 1942 waterhyacinth had spread into Mozambique to the Incomati estuary from N'ito Lurio to Jacoana and apparently originating from the Transvaal of South Africa (Wardlaw 1944). Korpaschuk (1948) indicated that waterhyacinth was already present in Zaire (the Belgian Congo) in the Congo River in 1924. Costa (1958) felt that it was introduced in the period between 1948 to 1949. Other authors (Beck 1944, Giles et al. 1944) 1944-1950 for its introduction into the Congo. By 1950 it had spread over 1000 km of the river between Leopoldville and Stanleyville (Korpaschuk 1958). Day (1962) first observed waterhyacinths occurring on the White Nile of the Sudan in 1955 along about 1000 km. It was apparently not abundant in the river prior to 1962 although it may have been present in 1954.

Senegal first reported the presence of waterhyacinth in 1944 (Gougeons 1944) from the Cape Vert peninsula and this may perhaps be the first record in the northwestern part of Africa. In spite of the surveys supported by the Inter-African Phytosanitary Committee it was still available for purchase from street vendors in Senegal in 1965.

Waterhyacinth is now distributed in all of the tropical and subtropical areas of the world. Its northernmost fields of distribution are probably near Sacramento, California (Laf. 36, 37 S, Beck 1942).

the Potomac River near Washington, D.C. [ca. 38°N; Goodrich and Hickey 1949; G.L.B. & 1950], Japan [36-38°N, note ... et. 1981] and possibly Portugal [35-40°N] as indicated by Sade et al. [1981] on their distribution map. The southern most limits of distribution appear to be Buenos Aires, Argentina [34°S] and Concepcion, Chile [37°S] in South America [Davis-Laurin 1984], and Skaneateles, New Zealand [46-47°S; Anonymous 1981]. The range in general seems to be bounded by the 40° North and South latitude lines. Very little information is available on the altitudinal restrictions of this species although one paper [Anonymous 1982] states that it is limited to the tropics to an altitudinal zone of from sea level to 6000 feet (ca. 1800 m).

### Sublitas

Little is known of the ranges of environmental tolerances of *sublitas*. Weber (1982) noted the effects of freezing temperatures in Florida in the winter of 1984-85. He noted that the first freeze killed the top which caused the plant to float higher in the water. A second freeze killed the newly exposed portion. Most of the plants survived by resprouting from the submerged portion of the rhizome.

Isakson and Co. (1983) stated that temperatures as low as 39°F (-1.1°C) may be withstood by the roots but will kill the tips. Temperatures lower than this will kill the roots as well. Probst et al. (1980) observed *sublitas* subjected to two days of freezing in New York. The plants were ice-covered when transferred to the greenhouse. Damage was apparently severe as the authors noted that all the foliage and all the roots were killed. Within 13 days the plants had recovered by resprouting from the rhizome tip. Myers (1984) placed

plants in a desiccator at  $-30^{\circ}\text{C}$  for 3-8 hours and they failed to revive. He found that at  $10^{\circ}\text{C}$  the growth became restricted and the plant did not show any increase in growth up to a 30-day period.

Freeland and Lurie (1955) exposed small plants in trays with 3 inches of water to various air temperatures for various durations. They found that at  $12^{\circ}\text{F}$  and  $27^{\circ}\text{F}$  ( $5-36^{\circ}\text{C}$  and  $-2-28^{\circ}\text{C}$ ) all of the rhizomes resprouted when returned to room temperatures after being exposed for 12, 24, and 48 hours. At  $12^{\circ}\text{F}$  ( $-4^{\circ}\text{C}$ ) all resprouted after 12 and 24 hours but none survived after 48 hours. At  $27^{\circ}\text{F}$  ( $-2-11^{\circ}\text{C}$ ) none survived 12 hour exposures but some survived 24 or 48 hour exposures. At  $10^{\circ}\text{F}$  ( $-7-10^{\circ}\text{C}$ ) none resprouted after being exposed for 12, 24, or 48 hours. They concluded that the temperature effect depends upon the duration of exposure and that freezing of the rhizome tip results in the destruction of the plant.

Stokess, et al. (1955) found that satisfactory growth occurred in air temperatures of  $25-27^{\circ}\text{C}$ . D'Haeseleire, et al. (1955) stated that the plants grew well in water temperatures ranging from  $17-26^{\circ}\text{C}$ . Cook (1955) measured air temperature ranges of  $17-26^{\circ}\text{C}$  and water temperature ranges of  $13-21^{\circ}\text{C}$  during the waterhyacinth growing season and water mid-day temperatures of  $5-10^{\circ}\text{F}$  for air and  $5^{\circ}\text{C}$  for water in California. She also stated that the population survived the winter of 1953-4 from which the southern 25 is with air temperatures below freezing, 1954-5 with 25 day, and 1955-6 with 18 ds although considerable mortality did occur.

Edgington et al. (1959) measured waterhyacinth growth along a gradient of water temperatures. They found the optimum to be  $25-30^{\circ}\text{C}$ .



although relatively high growth occurred over the range of 22-25°C. Exposure to 12°C nights reduced the amount of photoperiodic leaf-folding over days.

Book (1984, 1985) exposed plants to 26.1°C-26.2°C, 26.2°C-4.4°C, and 4.4°C-4.4°C day-night temperatures under both 18-18 and 8-16 L/D photoperiods. She found that growth was favored by the higher temperatures although it also appeared to be favored by the shortened photoperiod.

The maximum tolerable water temperatures appear to be around 22-24°C. Pothof and Gail (1944) observed that the plants showed tolerable water temperatures above 24°C. Book (1985) stated that in Gail's the plants succumb at water temperatures above 22°C. Kelping et al. (1976) found that growth began to be inhibited at about 22°C and declined to a nearly 100% reduce at higher temperatures until, by 40°C, negative growth was indicated. They noted that the plants were more tolerant of lower than optimum temperatures than of higher than optimum.

Light relations have been investigated by a few authors. Pothof and Gail (1944) noted that in July the average light intensity was about 425 foot-candles above colonies of *Antennaria-silene* plants. Under the canopy of large plants the light intensity was about 115 ft-c representing a 60% decrease. They found that significant algalic lesions are formed at intensities ranging from 125-400 ft-c and plant lesions are formed at intensities over 280 ft-c. Under a willow where the light intensity was 135 ft-c (34% of the July average) most of the plants were found to be dying. They also placed containers of *Antennaria-silene*

under a table where the light intensity averaged 80 ft-c and all of the plants died in 2 mo. In connection with this they placed several plants in the dark and measured the starch depletion. By 7 d the starch content was reduced by 60% and by 12 d it was completely gone.

Wickstead et al. (1944) grew plants in a greenhouse and supplied one group with supplemental heat, one group with supplemental light, and one group was left as a check. They found that the no. leaves per plant, the average leaf length, and the no. flowers produced were greatest in the high light condition.

In Africa (Adegoke 1957) it has been noted that light is seldom a limiting factor with respect to vegetation and fructification but it may have a more direct influence on germination.

As previously mentioned our study (1944-1945, 1948) found that plants grown under the same temperature regime grow better under the shorter photoperiod. This peculiarity was not explained.

Wick (1940) stated that watermelons under 600 full sunlight or better although they failed to develop full sunlight. She placed plants under greenhouse benches where the light intensity at noon was 80-400 full sunlight. These were harvested there from September to March and 47% mortality was observed.

Went (1927) subjected plants to 400, 500, and 1000 ft-c light (approximate) and found that the no. leaves per plant and the percentage leaves with flowers increased with increasing light intensity. Correspondingly a reduction in the average volume and diameter of the fruit occurred as the light intensity decreased.

Kodiyang et al. (1986) measured net productivity of attached leaves under a range of light conditions. Photosynthesis increased from  $2.9 \text{ mg CO}_2/\text{hr}^2$  leaf surface/yr to  $16.1 \text{ mg/hr}^2$  at the light intensity increased from 1400 ft-c to 5000 ft-c. Root respiration was found to range from 3.4 to 3.8 (average 3.7)  $\text{mg/hr}^2$ .

Waterhyacinth is generally considered to tolerate a wide range of pH (Petersen 1970). Heller and Latta (1972) found they grew over a range of 4.0 to 10.0 although optimal growth occurred in soil to slightly alkaline conditions (4-8). Both (1988) using data from other authors concluded that waterhyacinth generally occurs in waters ranging in pH from 4 to 9. Goodrich and Shand (1980) compared the growth of waterhyacinth and water lettuce (*Pistia stratiotes* L.) in cultures of varying pH. They found that waterhyacinth would grow at all levels (pH 3.0 to 9.0) but at 3.0 both dry-weight yield and offshoot production were minimal. They felt that pH values near 7.0 were optimal for waterhyacinth but values near 8.0 were optimal for water lettuce. Redfern and Karle (1980) reported pH values usually ranged between 6.5-8.5 in or near waterhyacinth mats in Louisiana but could survive extremes of 4-5 and 9-10. In the Sahelian region of Africa pH is thought to be fluctuating at values of 6.0 or below (Jong 1980, Kodiyang 1987).

Minchall and Scott (1961) studied the effects of the ranges of pH (3-9.0) on the roots of waterhyacinth. They found that at values below 6.0 the roots exhibited decreased cell division and cell elongation (cell division at pH 6.0 proceeded faster as fast as at 8.0). They further found that the plants could tolerate more acidity at cooler temperatures and the pH of the cell sap was always more than that of the culture medium.

A few authors have suggested that stands of waterhyacinths may modify the pH of the water. Forthum and Carls (1960) noted that pond waters in the Mississippi River delta have an average pH of 7.2 whereas water in waterhyacinth beds are usually acid. Blich (1933) compared open water areas of a pond with areas covered with waterhyacinths and determined the yearly average pH to be 5.6 in the open areas and 5.4 in the areas with waterhyacinths. Butler and Butler (1933) presented data which indicated that the plants cause a change in the direction of neutrality from both high and low initial pH values. Carter and Kalschauer (1949) compared water quality parameters from sites with and without waterhyacinths and found that those with the plants had lower pH (7.00 to 8.0) than those without (7.50 to 8.0) although the difference was not significant.

Moisture requirements of waterhyacinths and the effects of desiccation upon its survival and growth have been only superficially examined. Mosler (1937) noted that if the plants are to succeed a soil of loose texture thoroughly saturated with water is required. Forde (1940), however, found that they could survive a 75% of water saturation in soil. Beck (1940) noted one instance when the plants survived 44 days in saturated soil. He speculated that the plants can withstand periods of desiccation because extensive transpiration is prevented from the center of the rosette by the protective layer of dead water leaves. Forthum and Carls (1960) found that waterhyacinths could survive drying periods up to 18 days depending upon climatic conditions and the surface they are exposed to. Long weather with the plants on gravelized sand killed the plants rapidly while rainy and cloudy weather or placing the plants in the

shown at least that to survive longer. Brown (1960) found that when the releases are air dried they progressively lose the ability to respond as the moisture content decreases. They can tolerate a lower moisture content when dried in soil, however, than when dried in air. This may enable them to survive droughts in some habitats.

As far as I have been able to determine back (1960) is the only one to have investigated the effects of humidity on the growth of waterhyacinths. She grew plants in a growth chamber both inside a plastic enclosure with high humidity and outside the enclosure. She concluded that high humidity favors growth.

With the recent interest in the utilization of waterhyacinths for nutrient removal, it seems efficient. Increasing attention has been directed towards the nutrient requirements of this plant. Spedal (1960) found that the plants grow in both nutrient-rich and nutrient-poor water and that the nutrient content of the plant was higher in nutrient-rich water. Michelson et al. (1960) suggested that waterhyacinths have relatively low nutrient requirements as good growth occurred in solutions 0.01 to 0.001 times as strong as normal in water culture. They also found that the growth response increased with added nutrients.

In Africa (Jongman 1967) it has been noted that the lower limit of "hypernitration" is very low but little is known of the upper limits. Dethlefs and Burke (1966) found that an increase in nitrogen levels caused a linear decrease in the total yield and plant number but had little effect on the mean weight per plant. Rejzling et al. (1965) studied two sites with widely different levels of orthophosphate and were surprised to find that the average floating crop yields were

similar at both sites. They further found that plants grown in varying phosphate solutions ranging from 0.05 ppm to 2.40 ppm did not significantly differ with respect to percentage weight gain over a 17 day period. Ballan, et al. (1955) found that the critical phosphorus concentration for waterhyacinth growth was 0.51 ppm. Above this level phosphorus was absorbed in luxury amounts but a higher proportion of that available was absorbed at low concentrations. Miller and Sutton (1931) found that optimal growth occurred at 50 ppm phosphorus but levels higher than 40 ppm were toxic. They further found that the root weight was greatest at 2 ppm reflecting a tendency towards maximizing root absorptive surface in response to low nutrients.

Sutton and Blackmore (1936, 4) investigated the effects of varying copper solution on growth and transpiration of waterhyacinth. They found that transpiration was reduced at 1.0 ppm with copper when grown in the solution for 1 week and at 2.0 ppm when grown for 2 weeks. Growth was inhibited by 0.5 ppm when subjected to the solution for 2 weeks. After one week the total dry weight was reduced at 0.5 ppm or above and the root dry weight by 16.0 ppm. The copper content of the shoot reflected the content of the water when the concentration was above 2.0 ppm but at levels below this the concentrations in the roots were independent of those in the water. The copper content of the roots increased linearly with the solution concentration.

Engel and Scarborough (1953) found that the addition of 20.32 g  $\text{KH}_2\text{P}_2\text{O}_7 \cdot 8\text{H}_2\text{O}$  fertilizer to ponds increased the biomass yield of waterhyacinth. The fertilizer was added at 4 levels 0, 0.2 kg/ha, 10.4 kg/ha, and 21.8 kg/ha. It was interesting to note that the highest level of fertilization resulted in a yield less than the two intermediate levels.

## Community Associations

Because of the worldwide distribution of waterhyacinths any comprehensive list of plants associated with it would be a tremendous task. A few authors have treated this subject on a local level, however. Reager (1934) noted the association of an orchid, *Salweenia repens* Nutt., with waterhyacinths in Georgia. Noel (1938) listed a dozen plants which may be found growing on the floating mats of waterhyacinths and noted in his opinion that it grows tentatively with several other aquatic species. Redford and Redkey (1938) described plant communities in the marshlands of southeastern Louisiana. They found waterhyacinths associated with the cypress-gum swamps in slightly fresh water and presented an extensive list of other associated species. Redford and Lurie (1940) found a tremendous array of plants (31 species) occurring on mats of waterhyacinths. Taylor (1940) investigated the effects of 2, 4-D on other plant species associated with waterhyacinths and algal growth. Cardwell and Smith (1944) investigated relationships between *Potamogeton nodosus* and *Salicornia virginica*. Roth (1944) listed several species associated with waterhyacinths in California and reviewed the work of several other authors. Alm-Christi and Yacobi (1954) noted the composition of the phytosoc community in association with waterhyacinth stands in the Delta.

Several workers have reported on the fauna associated with waterhyacinths but this has largely been the result of biological control investigations dealing primarily with insects. Myers (1937) tentatively listed the fauna associated with waterhyacinth stands. Hansen et al. (1937) listed some invertebrates present in the aquatic component of the waterhyacinth community and constructed a partial food web. They also studied the invertebrate present on old mats (1940).

The naturalness of watergrubs in water large and rivers. Most of the information available regards those species which feed upon water-grubs and, thus, have potential as biological control agents. Bennett et al. (1988) investigated a grasshopper (*Acrida poae* (Forsk. (Orthoptera: Acrididae)) attacking watergrubs in Texas. First Bennett et al. (1988) has published many reports on the possibility of biological control of watergrubs and on the insects associated with it (Bennett 1987, 1988a, 1988b, 1988, Bennett and Beiffer 1988). Other data have been provided by Jones and Carlson (1984), Carlson (1979), Perkins (1978, 1984) and Spencer (1983, 1984).

Salcedo (1974) described a dipteran (Diptera: Chironomidae: Chironominae) from South America. Warner (1970) investigated the growth and assimilation efficiencies of an insect (*Chironomus albigaster* which is known to feed on watergrubs. Stiles-Gale and Perkins (1983) reported on the biology and host specificity of *Chironomus aquosus* (Brund.), a grasshopper (Orthoptera) from Argentina which attacks watergrubs. Salcedo (1983) provided identification and biological notes on the genus *Chironomus* (Chironominae: Chironomidae) that attack the freshwater in South America. Salcedo and Costa (1984) provided information on the life-cycle and biology of *A. chironomus* and *A. lewisi*, two species which have been released for the biological control of watergrubs in the United States. Warner (1970) described these two species.

Salcedo (1983) described a leaf-feeding psyllid (Homoptera: Psyllidae: Psyllinae) from Uruguay which feeds on watergrubs which has previously been found in the United States (Bennett 1988a). Perkins (1983) studied the biology and host specificity of this species in Argentina.





layer of lacunae (tissue) is between. The perianth whorls is surrounded by a weakly differentiated endostoma and peristoma (Cough 1970). Limited meristematic activity occurs at the apex and the roots possess a distinct apical meristem (Haultboeue 1967). The roots are known to become embedded into the mud although they are usually suspended freely in the water (Hultine and La 1980, Smith 1984, de Vries 1986, Poffenb and Dar's 1988, Poffenb 1989). The color of the roots is normally dark violet blue due to the presence of anthocyanins but when growing in the mud or in the dark the roots become white (Olive 1984; Poffenb and Dar's 1988). The roots arise from nodes on the rhizome (Poffenb and Dar's 1988).

The rhizome is the vegetative stem of the plant from which all other structures arise (Poffenb and Dar's 1988). It consists of an compact area with short internodes and the leaves, roots, stolons and inflorescences are produced by the meristematic nodes which have generally small, compact cells. An area with a considerable number of intercellular air spaces exists around the periphery of the meristematic tissue (Smith 1981). The rhizome is approximately 98% water by weight and has a specific gravity of 0.985 (Poffenb and Dar's 1988). Olive (1984) indicated that there was no evidence of starch being stored within the rhizome (criticized but Poffenb and Dar's 1988). Poffenb and Dar's (1988) felt that the rhizome was the main organ of starch storage.

The rhizome may produce long horizontal internodes (stolons) which produce new shoots at the distal end which results in a typical branching pattern (Poffenb and Dar's 1988). These stolons arise from axillary node buds (Stock 1986). Aerial top sprouts are situated near the periphery and the inflorescent bundles are aggregated to the center (Olive 1984). The stolons are purple due to the presence of anthocyanins and range in diameter from 0.5-2.0 cm  $\times$  1' length up to 40 cm (Poffenb 1989). The

specific gravity of the stipe is 0.88 and is constant at about 0.71 water by weight (Postland and Davis 1948)

The most interesting morphological development of the waterhyacinth is its leaves. Jester (1911, 1928) found that the vascular bundles in the petiole are arranged with the xylem oriented towards the periphery. There is the lamina may be arranged with the xylem up, down, or oblique. This is in contrast to plants with a true lamina which have the vascular bundles arranged with the xylem towards the upper leaf surface. She suggests that this indicates that the lamina is merely an extension of the apical end of the petiole and not homologous with the lamina of a *Claytonia*. As such it should properly be called a pseudostem and the basal portion a petiole. The two are connected by a narrow conical region called the influen and the narrow base below the float is referred to as the subfloat. A continuous ligula (= stipe of Jester 1914) is present at the base of the subfloat (Postland and Davis 1948) which possesses a small verruca lancea (Spillard 1924).

The petiole may be more or less inflated to form a bulb-like structure commonly known as float or floating-the-plant (Parsons 1944, Adams 1927, Gifford and Leigh 1921, Ellis 1924, Cook 1921). This has been contradicted by Lee (1950a) because the blades are found mostly above the water and the leaves float with or without them. Lee (1944) noted, however, that the bases of the inflated petioles just beneath the water formed a stable platform. Further, floating single plants with elongate petioles were unable to remain upright and if they remained on their side and not grow leaves with inflated petioles.

Several factors have been indicated as important in the development of the float. Jan (1936) concluded that high osmotic pressure was the important factor although this may be altered by numerous factors. The lack of swelling may also be associated with high plant density (Lalonde 1935), exchange to salt (Lalonde 1935, Nelson 1937), shade and high temperatures (Lalonde 1935, Arner 1939). Conversely, hollow petioles may be associated with the free-floating habit, full sunlight, or cooler temperatures (Lalonde 1935). Beck (1944) found she could not correlate petiole shape with shading.

The buoyancy of the plants is largely due to the presence of air spaces in the highly incised parenchyma resulting in 90% air by volume (Nelson 1937). The average gravity of the float is 0.106 and of the parenchyma is 0.141. The floats are 90% water by weight and the parenchyma are 85% (Sherwood and Earle 1948). The petioles range in size from a few centimeters to as much as 1.5 meters in the upright form (Hickman and Is. 1950). The angle between the leaves and the water surfaces ranges from 15 to 45° around the periphery of the rosette and from 75 to 90° in the center (Sherwood and Earle 1948).

The leaves not only stabilize the plant and keep it afloat but act as sails which catch the wind and give impetus of them over the surface of the water (Nelson 1937, Is. 1938). Further, the geometric arrangement of the leaves into a rosette with a large leaf area (as much as 8 m<sup>2</sup>/m<sup>2</sup>) and the erect habit of individual leaves is extremely efficient for light interception (Schilling et al. 1958).

The structure of the parenchyma and petiole is further discussed by Olive (1944), Beck (1944), Scott-Sherwood (1967), Arner (1915, 1939),

and Panchang and Earle (1944). The ligular system may enclose the plant in certain temperate eastern species (Wittings and DesFrip 1947).

The inflorescence is displayed on a long peduncle (Panchang and Earle 1944) and is usually elevated a few centimeters above the leaves (de Tili 1938). Two opposite spathe subtend the inflorescence the lower being leaf-like and bearing a pseudanthium and the upper bract-like (Cook 1974). The inflorescence is a spike (de Tili 1938, Buckner and Co. 1958, Panchang and Earle 1944, Cook 1943) or may be considered spike-like or paniculate (Cook 1974, Cook 1966). The spike is 10-20 cm long (de Tili 1938, Rose and Fernald 1934) and contains numerous flowers (4-40, de Tili 1938, 5, Fernald 1943, 10-12, Pilgum 1933, 4-12, Rose and Fernald 1934, 4-19, Ryan 1938) borne on a rachis with a flower/leaf sub-nodus below the inflorescence and above the spathe (Panchang and Earle 1944). The individual flowers consist of a hypanthium about 1.4-1.8 cm long (Hara 1943), 3 sepals, 3 petals, 6 stamens and a triloculate ovary (Panchang and Earle 1944). The petals and sepals are broader in color (Cook 1966) and united at the base to form a 6-lobed tube (Cook 1974). The color of the flower is due to the anthocyanin, cyanidin (Hidaka et al. 1964). The tube is curved, glandular and pubescent near the base (Rose and Fernald 1934). The perianth is slightly irregular with all 3 sepals and 3 petals similar in size and shape but the upper petal is somewhat wider and bears a distinctive yellow spot in the center bordered by a darker blue or violet area (Cook 1966, Buckner and Co. 1958). Buckner and Co. (1958) indicate that the function of this spot is unknown but others have indicated that it may function as a nectar guide to visiting bees (Smithberger 1947). The six stamens are arranged in two

stems of 3 stems each, of two different lengths and are always being fixed to the corolla tube at the base of the filaments near the insertion of the perianth tube (Hook 1944). The filaments are white at the base, purple at the apex, and glandular (Peters 1931). The anthers are oblong and attached near the base (Hook 1944) and contain about 2000 pollen grains each (Purdum and Lurie 1948). The ovary is superior, sessile, trilocular, contains numerous ovules in axile placentation (Nelson 1931, Hook 1944) and is covered in scales (Purdum and Lurie 1948). The six stigmatic surfaces, by their close apposition, appear to be confluent but they are not (Purdum and Lurie 1948, Hook 1944). The stigmate surface is covered with numerous glandular hairs (Hook 1944). The fruit is a loculicidal capsule containing seeds with an abundant oily endosperm (Nelson 1931). Approximately 50 seeds are produced per capsule (Purdum and Lurie 1948).

### Reproduction

Waterbury (1941) is generally considered to be a pioneer in studies of the rhizome (Purdum and Lurie 1948, Gentry 1961). Purdum and Lurie (1948) felt that the rhizome may maintain a constant length over a period of several years. Exact data on how long an individual rhizome may exist is not available but the plants are known to survive periods of freezing weather by resprouting from the rhizome (Hook 1944).

### Ecological Data

Much of the appropriate physiological data has already been discussed in scattered sections of this literature review but it seems appropriate to have organized discussion:

Many authors have studied transpiration rates and found variations due to such factors as solar energy, wind speed, temperature, and hydroponic flats. (1961) found that water loss through a waterpouch flat was as high as 15.5 kg/m<sup>2</sup>/hr. This represented a water requirement of 4.74 kg of water per gram (dry wt %) of biomass produced. The ratio of evapotranspiration to open water evaporation ( $E_p/E_o$ ) ranged from 0.52 to 0.88.

Belting et al. (1974) measured the moisture content of a stream of air before and after it had passed over a waterpouch flat. They found during the day the transpiration rate increased from 1000 to 2400  $\text{mg/m}^2$  (leaf surface)/hr in response to increasing light intensities. Dark transpiration values were also high, however, averaging 1400  $\text{mg/m}^2$ /hr. In another experiment plants were grown in buckets in a variety of phosphorus concentrations and measured for daily water loss. There was no significant difference in evapotranspiration between the phosphorus concentrations. The  $E_p/E_o$  ratio, however, was 300 g/m<sup>2</sup>/100 g/m<sup>2</sup> or 3:1. Dry matter production was 0.07 g/m<sup>2</sup> indicating a water use efficiency ratio of 1425  $\text{mg H}_2\text{O/g plant dry wt}$ .

Other average values reported for the  $E_p/E_o$  ratio have been 1.2 (Overland and Davis 1968), 2.8 (in leaf) (Nelson et al. 1961), 3.3 (Timmer and Welfos 1967), 1.52-1.56 (Greening et al. 1972), and 1.46 (Fox and Short and Kramers 1974). The latter authors have found that 5% of evaporation from waterpouch covered solutions is the result of the process of evapotranspiration.

Calvin et al. (1970) have also provided data on respiration and photosynthesis by measuring the  $\text{CO}_2$  concentration in an air stream passed over a flat. Net photosynthesis increased from 2.8 to 18.1  $\text{mg CO}_2/\text{m}^2/\text{hr}$

with light intensities increasing from 1440 ft-c to 8000 ft-c. Respiration averaged  $2.7 \text{ mg } \text{CO}_2/\text{gm}^2/\text{hr}$ . Vitousek and Anthony (1971) have found that *Spartocytisus* may have the capacity to utilize  $\text{CO}_2$  dissolved in the water under the best of a range of carbon to respiration through the roots. This gas would be up to 10% of the total carbon fixed. Hitting and Lindsey (1967) have found that some leafless shrubs plant may use internal carbon dioxide generated from root and stem respiration in photosynthesis. This may be true in the case of *Spartocytisus*.

Quantitative uptake rates are not well worked out for this plant. *Spartocytisus* contains about 3.45 P and 3.80 S by weight (dry 1950s) or on a S-P ratio of 1:1. If these represent constant proportions the rate of nutrient uptake is proportional to the growth rate of the plant. If the standing crop increases at a rate of 100 g/m<sup>2</sup> the rate of uptake of S will be 3.4 g/m<sup>2</sup> and of P 0.4 g/m<sup>2</sup>. This agrees well with the results of Jørgensen et al. (1975) who found the S-P ratio of uptake rates to be 1:1. The daily absorption rates from 6 liter containers were 2.4 ppm S and 0.4 ppm P in water concentrations of 50 and 100 ppm S and P. At concentrations of 240 ppm S and P the daily uptake rates were 3.5 and 0.7 ppm respectively. This implies a growth rate of 600 and 650 mg dry uptake. Vitousek (1975) indicates that this high value of S-P absorption indicates that nitrogen is generally more limiting to *Spartocytisus* than phosphorus.

### Discussion

Data on the sequence and timing of events in the annual cycles of *Spartocytisus* populations are scarce. Harford and Dorte (1988) estimates the average length of the longest leaves over one growing season. The



maximum was reached in August and the period of maximum growth was between May and August. They also followed the flowering cycle over a period of years in Louisiana. In the years 1845-1847 authors began in April, they felt that a definite flowering rhythm occurs in a given colony of plants. Anthesis is maximum in June and declines through September although this may vary from colony to colony and a second period of flowering occurs in September and October and continues through November into December. Burrows and Co. (1920) reported that the plant is supposed to bloom every two to three months. In India flowering occurs throughout the year but is most abundant in the post-monsoon months (Sahel and Shaha 1972). A pre-monsoon flowering period (April and June) has been reported in India (Pieris 1934). Sahel and Shaha (1970) further found that biomass accumulation was highest in January and February, and the area occupied by vines was greatest in February and March in India.

### Reproduction

#### Floral Biology

A single flowering spike contains a variable number of flowers. Beck (1944) found the average to range between 5 and 10 flowers per inflorescence although she indicated that other authors have observed up to 20 flowers per inflorescence. Smith (1936) indicated that flowering occurred on a daily cycle starting as buds up to 7:00 AM and opening by 8:00 AM. The mode of pollination may be allogamous or autogamous. Beck (1944) found that allogamous pollination may occur through the action of several insect pollinators, the Titled *Apis mellifera*, *Andrena* (C. sp.), and *Colletes* (C. sp.) as known pollinators and several flies as possible

pollinators. Aschmann and Corla (1961) observed hemiparasitism, both within and between species, but neither butterflies visiting the flowers. They described three patterns of behavior of hemiparasites in visiting the flowers: visiting distal anthers only, alighting with the head among the proximal anthers and the stigma on the style, and visiting the proximal anthers after alighting on the lower point. They questioned the importance of insect pollinators in accounting for the production of seed in this species. Beck (1966) noted, however, that hemiparasites crawl down the floral tube to retrieve the nectar and in so doing receive pollen from both sets of anthers. She observed a great deal of cross-pollination.

Autogamous pollination occurs when the flower wilts and the stamens are twisted against the stigma (Aschmann and Corla 1961, Beck 1966; Fox et al. 1961 and Corla 1975). Aschmann and Corla (1961) found much more pollen on the stigma after the flowers had completely wilted than at any other time thus stressing the prevalence of autogamous pollination.

Since entopterygids flowers are at least dimorphic with regard to style length either hypostylate (styles pollinated by anthers not of equivalent length) or litigylate (styles pollinated by anthers not of equivalent length) crosses are possible (Aschmann 1966, Beck 1966, Douglas 1964-65). Both litigylate and litigylate crosses result in seed production (Beck 1965). Douglas's (1964-65) reported that self-incompatibility was stronger in long styled forms than in short styled forms. Brinkoff (1966) studied the breeding system of *Aspidosiphon axillaris* and compared it with *A. conopsea*. He concluded, as did Beck (1966), that both species exhibit relatively weak self-incompatibility.

An interesting aspect of the floral biology of entopterygids is the

placement of anthesis/ovis at the heading of the culm of the inflorescence following anthesis (Agharhar and Ismail) (1935, Lalanda 1933, Boland 1933, Asfand and Ismail 1940, Bala 1940, Malik 1961). Lalanda (1933) described this process as follows:

"As soon as the inflorescence starts willing the upper portion of the culm with the fertilized glumes begins to bend forward. When this upper part has reached the surface of the water, usually after five days, the lower portion of the culm commences to bend at the base, thus pushing the developing seed-pods under the surface of the water. This movement stops when the lower part of the culm is level with the surface. The upper part carrying the seed pods is then submerged in the water at an angle of 45°, the seed pods being covered and protected by the rest of culm . . . The whole process of heading requires from six to seven days." (Lalanda 1933, p. 31)

Agharhar and Ismail (1935) quoted other workers who indicated that anthesis/ovis was accompanied by a lengthening of the peduncle. They found, however, that the peduncle did not lengthen considerably and such lengthening was confined to an area of 1 to 2 cm below the terminal node. They further found that removal of the flowers or abscission of the peduncle above the node had no effect and curvature was normal. This was also true when they removed the culmlets and placed it in water.

Asfand and Ismail (1940) stated that anthesis/ovis cycle and their results agree with other workers. They found that it requires about 14 days from the initiation of the floral bud until opening occurs. Floral opening begins about 4:00 PM, if all the flowers open the heading phase begins at about 4:00 PM of the same day. Heading occurs in three places at the rhizome crown, *i.e.* above the two internodes of the inflorescence,

and in the rocks. Most of the flowers are inserted by 3.00 PM the following day. The complete cycle from flowering to complete germination takes 48 hours in the summer. This is contrary to Leland's (1930) finding that it takes 4 or 7 days. Beck (1955), in her studies, agreed with Hefland and Clark (1944).

Beck (1955) seemed to concur with the findings of Day (1934a) in that the heading was due to geotropism in that when the roots were packed with sponges and the plants held horizontally, no heading occurred. She disagreed with Lohman and Bauer (1938) in that removal of the flowers would not permit heading to occur unless all of the flowers had withered and heading had commenced first.

Beck (1955) found that curvature took place when the tips along with 2 terminal flowers were removed, when all of the flower buds were removed, and when all of the flowers were removed after they had opened. In all cases complete heading took as long as in the controls (20-48 hrs.) She found that this curvature was due to increased cell size along the outer edge of the curling portion. She felt that this process represented a free-running endogenous rhythm independent of auxins (geotropic in nature), photoperiod, temperature, and opening of the last flower as suggested by other authors.

Gymnogenesis has been described by Smith (1936) and Kasevich and Kasevich (1937) and *hypogaea* by Smith (1936). Pollen morphology and germination and development of the pollen tube have been investigated by Kasevich and Kasevich (1937), Beck (1944) and Tag et al. (1954) and Smith (1936). The morphology of the seed is discussed by Smith (1936), Kasevich (1937), and Bailey (1954).

### Seed Production and Abortion

The degree of seed set seems to be extremely variable. Agarwal and Senyál (1958) found that 12 hours after anthesis through natural pollination (autogamous or allogamous not distinguished) 25% of the flowers were fertilized (25% with actively growing pollen tubes and another 50% with pollen grains present). Through artificial pollination, up to 75% of the fertilized flowers set fruit. Bhatia (1953) in Nepal found that only 7% of the flowers set any seed. Singh (1958) found in Ceylon that 36 to 77% of the capsules produced may be empty. Becker (1964) found an seed set in Java and Moore (1965) found up to 50% of the fruits were seed in India.

The conditions for seed set have been investigated but the results are confusing. Barja (1954) indicated that temperatures between 24°C and 28°C were necessary. Agarwal and Senyál (1958) felt that relative humidities above 90% were required. Beck (1965) found that seed was set when the relative humidity was never greater than 77%. Singh (1958) found the number of seeds per inflorescence to be 0%, 25, and 50 when the relative humidity was 50%, 70%, and 87% respectively. Tag et al and Sheth (1959) concluded that seed set was favored if pollination occurred immediately after the flowers opened. Therefore, successful pollination was hindered by high temperature and low humidity which affected the stickiness and receptivity of the stigma.

Data on the quantity of seeds set per fruit or inflorescence also indicate a great deal of variability. Singh (1958) artificially pollinated flowers and found an average of 34 seeds/capsule with a maximum of 72. Beck (1965) reported the average in California to be 8.2 with a range of

1-18. Burns (1955) indicated that the average may be 15-45. Robertson and Hale (1955) found 50-150 seeds/capsule in Burma, Jaeger (1962) reported 3-150, and Hasegawa (1964-5) reported an average of 150 ± with a standard of 250. Tag et al. Seed (1972) reported an average of 50-65 with a range of 5 to 542.

The number of seeds per inflorescence depends upon the number of flowers per inflorescence and the number of seeds per flower. Beck (1964) indicated that the average number of seeds per inflorescence is 3-44 in California. Tag et al. Seed and Garb (1970) reported 1-5 capsules per inflorescence. Using the data from Tag et al. Seed (1972) for the average number of seeds per capsule (50-65) this equals to 145 seeds per inflorescence. Reithman (1967) indicated that a single spike may produce 1000 to 4000 seeds. Jaeger (1962) estimated that 45 million seeds may be produced per acre by medium sized plants. Penfold and Garb (1968) estimated a crop of 500,000 capsules/acre.

The mode of seed dispersal has not been studied to any extent. It seems apparent that since the seeds are deposited in the water the primary mode of dispersal would be through drifting. A few authors have indicated that birds and foraging animals may disperse seeds (Oksanen et al. 1969; Hale et al. 1969; Roy 1969).

#### Viability of Seeds and Germination

Conditions for germination of waterhyacinth seeds have been studied by many workers. Greider (1967) refuted the idea of earlier workers that stratification of the seeds is a necessary prerequisite to germination. He further found that green seeds kept at 22°C germinated [100 within 1 week] while seeds kept at 4°C did not, although they did

Plum. Seeds with mature coats failed to germinate when kept at either 25°C or 20°C. He then separated the embryos from ripe seeds or ruptured the seed coats and placed them in a bath at 25°C. He noted that germination occurred very rapidly in both cases. (80% after 1 day). He noted wet oxygen as a factor because they germinated equally well in boiled water covered with paraffin. He concluded that the hard seed coat and endosperm hinder water absorption and inhibit germination and that desiccation may, in fact, fracture the seed coat and promote germination.

Agharwal and Banerji (1930) indicated that a ripening period of 10 to 25 days was required for maturation of the fruit. After maturation they are removed from the axis by an abscission layer and float on the water surface for a day or two before sinking. Apices develop on the lateral walls through which seeds are discharged. They found that the seeds develop freely in tap or distilled water.

Portia (1938) suggests that germination takes place "in the beginning of rains or whenever the humidity, soil moisture and temperature are suitable." (Portia 1938, p. 383). He felt that the function of the ribs was to provide moisture, and expose the seeds in the mud providing access to oxygen.

Robertson and Thain (1932) noted that in every instance when they had found water-soluble seedlings it was in a depression which completely dried out during the dry season and flooded again in the rainy season. They concluded that a period of drought alternating with a period of plentiful moisture was necessary for germination.

Baugh (1936) exposed seeds to varying treatments of always wet, always dry, or alternately wet and dry. No germination occurred for three months until seeds were placed in the sun. Within eleven days germination

led began. They further found that drying, including air in the water, and the addition of rotting submersible fragments would not promote germination when kept in the laboratory...To determine if heat or exposure to an intense light was the important factor they exposed seeds to a normal light both wet to a blackened light both. Germination occurred only in the illuminated treatment. They concluded that bright wet is necessary for germination and that heat, in conjunction with high light intensity may also be required. Raich (1960) later found that if stratification is prolonged for a long enough period light is not necessary. He found that seeds collected in June 1956 would germinate in the laboratory as late as January 1957 (19 months).

Radford and Lurie (1968) concur with Raich in his findings. They found that seed germination would occur on exposed plants indicating that either drying or increased light intensity was favorable for germination. They also concluded that scarification aided germination.

Stitchcock et al. (1964) indicated that an after-ripening period of about 2 months was necessary for germination and under these conditions 100% germination was possible. Dry seeds, however, required twice as long (111-112 days) to germinate as seeds stored wet (54-67 days). They also found that relatively high water temperatures (18-26°C) favored germination but the seeds could survive very cold temperatures. They stored for 60 days at temperatures of -5, 0, 5, 10, and 15°C and then placed in normal air temperatures. Germination occurred in every case except the -5°C treatment. When exposed for only 1 week even the -5°C treatment gave 50% germination.

Stitchcock et al. (1958) investigated the effects of water depth on seed germination. At water depths of 2.5, 10 L, 20 L, 30 L, and 40 L on they obtained 40, 60, 70, 70, and 100% germination respectively. They



felt that the difference was due to longer seed retention in the deeper water at night. Under 10.2 cm of water in a brown glass bottle only 28% germination was observed.

Baron and Hildebrand (1941) also studied the effects of temperature, light, and storage on seed germination. They concluded that a combination of high temperature and light is needed for germination of desert seeds although temperatures as low as 4°C did not impair germination when in direct sunlight (openness) and alternating temperatures (4-20°C, 4-25°C, and 5-40°C) allowed some germination even in the dark. They also found that a storage period of a month or longer hastened germination especially with less viable seeds.

Fraser (1944-5) obtained poor rates of germination (near 85%) by keeping his seeds in a 12/12 L/D photoperiod with a corresponding 40°C/20°C temperature regime. Bell (1964) was convinced that seeds do not germinate in California and found that they do not remain viable there for longer than 2 months. Gouillard (1967) reflected the findings of other authors by indicating that the seeds are able to tolerate a long dry period and remain viable. Day et al. (1972) investigated seed germination under a wide range of chemical treatments and under low oxygen tension and low water potential as well as many other environmental conditions. His extensive studies indicate that germination is stimulated by low water potential and low oxygen tension especially after wet strata, germination is most likely to occur in water warmed by intense light, the addition of organic matter to the substrate stimulates germination, the seeds will only germinate at the surface of the substrate, and aeration has no significant effect on germination.

The growth and development of the seedlings have been described by Pariza (1938), Robertson and Thain (1932), Seligs (1938), and Penland and Carle (1940). Several authors have indicated that a water saturated medium is necessary for seedling survival (Witchcock et al., 1940; Pariza 1938; Seligs 1938) but Robertson (1932) has noted natural growth of *S. flava* the seedling (Pariza 1938; Witchcock et al., 1940). Penland and Carle (1940) and Witchcock et al., (1940) noted that seedlings would grow in water-saturated flasks and Patten (1934) found them growing on the shore in "strand-lines" created by sand water-saturation. Witchcock et al., (1940) noted that in nature factors which prevent young seedlings from surviving may be more important than factors which permit seed germination.

#### Vegetative Reproduction

Even though seed production by water-saturation may be reliable, the primary mode of reproduction is through vegetative propagation (Witchcock et al., 1940). This occurs through the production of offsets, or suckers, produced as stolons (Penland and Carle 1940; Witchcock et al., 1940). They found that offset production begins about 60 days after the plant germinates when the rosette attains a diameter of 7.6 to 18.3 cm. Penland and Carle (1940) found that a root extends to boundaries at a rate of 3 feet per week through vegetative reproduction under favorable conditions and the plants double their numbers every two weeks. Both (1940, 1940) and Bentley (1937) have reviewed the literature dealing with the rates of offset production in different locations and situations.

#### Productivity and Seedling Grow

Many authors have dealt with water-saturation productivity in one

ture or another book (1984, 1991) has done perhaps the most comprehensive study on productivity but she dealt with fresh weights and biomass figures making comparisons with her data difficult. She also reviewed most of the literature on the subject and compared it to her data. Table 1 gives an updated compilation of various measures of standing crop and productivity of waterpockets from various sources.

### Control

The literature dealing with the various means of control is voluminous and I won't attempt to review it here. The *Specialist Control Journal* has been published annually since 1962 and is largely devoted to this subject. Furthermore, the various control methods have recently been reviewed. Bascom (1979) has reviewed the methods for mechanical control of aquatic weeds and Florkjær (1979) has reviewed chemical control and the various compounds available in a recent UNESCO publication in the same publication Baswell (1979) reviewed the biological control of aquatic weeds. Biological control has also been reviewed by Andreu and Baswell (1979) and the use of plant pathogens in biological control efforts by Iseliar and Freeman (1981), Freeman et al., (1984) and Dorelution (1985). Mitchell (1974) summarized techniques for the control of aquatic weeds through habitat management. McWhorter (1967) also discussed the various methods of aquatic weed control.



*Araneus domus* K&LTakenesque

Walton (1894) described three genera and three species of spiders in the family which are now known to be closely related. These were *Araneus atropus* (Heterobolusidae), *Araneus peripartus* (Heterobolidae), and *Araneus domus* (Derigidae). His description of the latter genus and species follows:

*Araneus domus*

**Male.** Body stout. Head with thick-set perfect hairs. Proboscis short, slender. Palpi stout, serrated, yellow, not extending beyond the hairs of the head, third joint extremely small, not more than one-fourth the length of the second. Anterior extremely pectinated, rather short. Anterior extending much beyond the third whip, tapering towards the tip, which has a very small tuft. Legs stout, rather short, first ending with a short fringe, spurs long, stout. Whips rather stout and narrow. First whips acute, anterior border almost straight, hardly oblique; second inferior vein almost as near to the third as to the first, fourth not very remote from the third.

*Araneus domus*

**Female.** Cephalic (subcapitulum) whitish and first whips reddish ochraceous. First whips with an oblique very broad brownish band, which contains the anterior and median marks, the latter are red, oblique, and narrow, a submarginell brown-bordered slightly dentate band, which is rather brighter than the ground but first whips beneath with a round brown spot in the disk, and

with a slight inferior brownish band. Length of the body 8 times, of the wings 16 times.

Grise and Robinson (1883) described a second species of *Aranea*, *A. albispina*. They considered this to be Walcott's type of *A. densa* in the British Museum and found they differed in the larger size of *A. albispina* and different coloration. They apparently failed to compare it with *Araneus albipes*, Simon.

Herrick-Sheaffer (1888. Cited from Ann. Record) provided generic and specific characters in part for *A. densa* from Cuba.

Grise (1891) described another species of *Aranea*, *A. undulipes*, which differed from *A. densa* Wlk. and *A. albispina* S. & S. primarily by its dusky yellow color. He also noted that it was less robust than *A. albispina* with the anterior wings more rounded posteriorly. Grise (1894) in his list of the Arachnids of North America listed only these three species but in 1913 (1914) described a fourth species, *A. clypeus* from Mexico. Goodrich (1895) redescribed *Aranea densa* Wlk. from specimens collected in Cuba. A fifth species, *A. melanopygia*, was subsequently described by Grise in 1911 (in Goodrich 1911) from Florida. He pointed out characters which separate *A. clypeus*, *A. undulipes*, *A. melanopygia*, and *Aphidius albispinus* (apparently a misnomer for *A. albispina* S. & S.) He noted that characters of the clypeus are of value in separating these two genera. In 1922 Grise synonymized *Araneus albipes* Wlk. with *Aphidius albispinus* S. & S. These five species were listed together in the subfamily Iruaninae by Grise 1931 who noted that the species with the black shield (i.e. *A. melanopygia*) is probably a variety of *undulipes*. Riley (1933) stated that the genus *Aphidius* did not so subspecies in nature and *Aphidius albispinus* S. & S. was synonymous with *A. densa* Wlk.

In 1888 Smith placed these species in the tribe *Arcturini* which included *Arctus* and *Spilota*, the former supposedly having a smooth front and the latter a tuberculate front. He considered *Arctus* as consisting of three species, apparently after having considered *A. melanopygus* to be a variety of *A. melanopus*. This was also how the group was arranged in his checklist of 1888.

Smith (1890) decided that Walker's *Arctus* and *Arctus* were composite and that Walker had given priority. He considered *A. dorsus* Wlk., *A. melanopus* Gt., and *A. melanopygus* Gt., synonyms of *A. portusolus* Wlk. He recognized *Arctus* *obliquus* Gt. as a *A. affinis* (Gt.). *Arctus* *obliquus* Wlk., *Spilota* *obliquus* (G. & P.) and *Arctus* *obliquus* G. & P. were considered synonyms of *Arctus* *obliquus* (Wlk.). Thus, the genus species were reduced to three, all in *Arctus* Wlk.

Rehnstedter (1892) redescribed *A. obliquus* (Wlk.) and *A. portusolus* Wlk. but he also recognized *A. melanopygus*. All three were found in New York. Holland (1900) considered *A. dorsus* (Wlk.), *A. melanopus* (Gt.), and *A. melanopygus* to be synonyms of *A. portusolus* Wlk. as did Smith (1900) but recognized the genus *Spilota* and considered *A. obliquus* (G. & P.) a synonym of *A. obliquus* (Wlk.). Karszen (1910) recognized the genus *Spilota*, by the single species *A. obliquus*, and *Arctus*. He considered *A. dorsus* Wlk. and *A. melanopus* Gt. synonyms of *A. portusolus*, and retained *A. melanopygus* and *A. affinis*. He also presented a key for separating the three *Arctus* spp.

Oyer (1913) revised the genus *Spilota*, described three new species, and he provided a key. He retained *A. obliquus* (Wlk.) and considered *A. obliquus* Wlk. and *A. obliquus* G. & P. synonyms. The new species described were *A. canescens* from Washington, D. C., *A. nova* from Florida,

and *A. pictipennis* from California. He also included *A. pictipennis* Say and indicated that the description of this species was on a forthcoming paper.

Fernald and Schunewolf (1904) considered *Aphidius* flet. synonymous with *Aphidius* Wlk. and listing *obliqueus*, *depressus*, *peripartus*, and *rossi* all species of *Aphidius*. They synonymized *A. depressus* Say with *A. depressus* Wlk. but made no mention of *A. pictipennis* Say. They considered *A. depressus* Wlk. distinct from *A. peripartus* Wlk. by virtue of a frontal protuberance. Later they described another species of *Aphidius* from New Jersey and named it *A. brevis*. In honor of its discoverer (Fernald and Schunewolf 1911).

Gravenhorst (1917) in a list of the insects of Florida recognized *A. peripartus* Wlk., *A. melanopus* flet., *A. obliqueus* Wlk., and *A. rossii* Say. Fernald and Schunewolf (1917), apparently having identified *A. obliqueus* for Gravenhorst, noted that they made their determination before the publication of Say's *A. rossii* and indicated that the specimens they identified were probably *A. rossii* Say. This is confusing, however, because here they are recognizing *A. obliqueus* Wlk. while they had earlier confused it with *Aphidius*.

Say (1912) re-evaluated the status of the genera *Aphidius* and *Aphidius*. He noted that Fernald (1904) placed *A. depressus* Wlk. as a synonym of *A. peripartus* as the assumption that both have a smooth clypeus. He also noted that Fernald and Schunewolf (1904) found that the type specimen of *A. depressus* Wlk. did have a tubercle on the clypeus and reconstructed the genus *Aphidius* taking *Aphidius* a synonym of it but considered *A. peripartus* Wlk.-distinct. Say examined several specimens identified as *A. peripartus* Wlk. and found that they all had tubercles on the clypeus and suspected that Fernald's types would also. In fact this would probably synonymize



*donus* Wlk., *parvipennis* Wlk., and probably *donus* Gyar. He therefore proposed the name *Araneopsis* for these species with a smooth front and suggested that *A. diffusa* be the type species and *A. melanopis* be included in the genus. He also described *Aranea melanomaculata*, a new species from Cuba.

Witt (1921) again considered all of these species in the genus *Aranea* Wlk. The species listed were *A. oblique* (Wlk.), *A. donus* (Wlk.) (= *macropus* Gyar.), *A. parvipennis* (Gyar.), *A. donus* (Gyar.), *A. melanomaculata* (Gyar.), *A. planifrons* (Gyar.), *A. parvipennis* Wlk. (= *melanopis* Wlk.), *A. melanopis* (Gylt.), and *A. diffusa* (Gylt.). He noted that *A. pallida* G. & S. and *A. lineata* G. & S. are probably races of *A. oblique* (Wlk.) but may be distinct species.

Conrath (1924) discusses this group of insects in his introductory entomology text. He noted that the genus *Aranea* contained three North American species, *A. melanopis*, *A. diffusa*, and *A. parvipennis*. He also recognized the genus *Aranea* and listed *A. oblique* as "one most common species". He included these species in the subfamily *Arachninae*.

Jones (1931) listed the macropterygids of British Columbia and included *Aranea oblique* (Wlk.) and *Aranea parvipennis* Wlk. He noted, however, that the latter species is a doubtful record. He synonymized Gyar's *Araneopsis* [nec.] with *Aranea* and described *A. melanopis* (Gylt.) a synonym of *A. parvipennis* Wlk.

Feltz (1932) listed *Aranea oblique* (Wlk.) and *A. donus* Wlk. from Pennsylvania. He considered *pallida* G. & S. a race of *A. oblique* (Wlk.), *oblique* Gylt. a synonym of *A. oblique* (Wlk.), and *macropus* Gyar. a synonym of *A. donus* Wlk.

Porter (1944) considered all species of *Asclepias*, *Artemisia*, and *Synedra* to be in the single genus *Artemisia*. He divided the genus into two groups based on whether the fruit was flat or had a strong central ridge. In the first group he included *parryana* Wt., *diffusa* Grt., and *velutina* Grt. and placed *velutina* Grt. as a synonym of *velutina*. In the second group he included *obliqua* Wt., *condens* B. & R., and *densa* Wt.

Shenck (1944) listed the Leguminosae of Florida and again recognized both *Artemisia* and *Asclepias*. He included *A. obliqua* (Wt.) J. (synonym B. & R.), *A. densa* Wt., *A. artem* (Gris.), *A. parryana* Wt., and *A. velutina* (Grt.). He noted that the two species of *velutina* were probably conspecific. He also referred to the specimen listed as *A. parryana* Wt. by Brunsbach (1917) and noted that it was actually *A. densa* Wt., making the former a synonym of the latter.

The only specimen listed by Thiele (1919) was *Artemisia parryana* (Grt.) Levens (1924) noted that *A. velutina* and *A. parryana* are separated largely by the color of their seed pods, the former being brown and the latter white. He found that dark brown seeded females (*A. velutina* Grt.) may produce white-seeded daughters (*A. parryana* Wt.). This indicates that *A. velutina* is merely a form of *A. parryana* Wt.

I received a personal communication from Dr. L. L. Todd from the Systematic Botany Laboratory of the U. S. Department of Agriculture in April 1954. He explained the taxonomic situation with regard to these species as follows:

I consider that *Asclepias* Miller 1804, type-species *A. parryana* Miller by monotypy is the valid generic name. *Artemisia* Miller 1804, type-species *A. densa* Miller by monotypy and *Synedra* Greuter 1879 (1876), type-species *Artemisia artemisia*

Banks & Robinson (-Robert Robinson Walker), I consider to be earlier synonyms. *Willow* has preponderantly more *drum* (Walker, 1904, List 1-1, pp. 32, p. 401 vs. p. 401), is antithetical, as far as I can find, J. B. Smith, 1903, Bull. U. S. Nat. Mus., No. 33, p. 381, was the first to treat both names and he placed *drum* in the synonymy of *Willow* (Walker, 1904, Cornell Exper. Stat. Rep. 328, p. 257-8, used *drum* in error, but divided the genus into two sections (Colossus and?) However, the character he used to divide the two sections are trivial. Members of *Willow* do not have single antennae as he indicates, and the frond may be developed in some forms. The extent of development of the frond is a character that needs more study. It will also be necessary to study the possibility that root plant variations are involved. I have indicated to others that I believe there are only two or three species in the genus, *periphrasis*, *obliqua*, and possibly *drum*. Smith believed that *periphrasis* and *drum* represented one species, and he used that latter as a synonym.

I think that it is apparent from the literature that the taxonomy of this group is of an uncertain status. I agree with Paul that these species probably represent one genus and the proper name of *drum* does not. In *Willow* does (25) is. Because of the widespread current use of the former name and the nature of a defective study in literature I have used the historical *drum* does (25) throughout this dissertation.

Table 2 lists host plant records for these species as indicated in various references. Because of the confusion created in the taxonomy of the group, however, these host records are not reliable. For example, Griesbach (1917) listed *Aspilota pergandeae* Wlk. from *Heliconella*, Florida, as indicated by Hagen (1924) and synthesized types. At the time, Cresson (1903), however, indicated that the *Heliconella* record quoted by Griesbach (1917) referred to *Aranea* alone. This creates uncertainty with the host record was not from Hagen (1924), who synonymized *Aranea* and *pergandeae*, but the ascription record was. Griesbach (1917) apparently derived the host record from other sources. It is therefore impossible to determine which species Griesbach's host record refers to. To partially alleviate this problem I have left the records in Table 2 with the material designated by the respective author intact regardless of synonymy. Where, in my opinion, there is sufficient agreement in the literature to indicate that a host is in synonymy with a more valid binomial, that species designation is included as a synonymy under the valid binomial.

Host plant synonymy also result in a great deal of confusion. For example, *Aspilota areolaris* (Pomp.) Miller & Standley listed as a host of *Heliconia volucre* (Table 2, No. 3c) is listed by Remington (1961) as a synonym of *Aspilota variegator* (Leprieu). *Aspilota areolaris* (Table 2, No. 3c) is also apparently a synonym of *Aspilota variegator* (Fassett, 1951). I do not believe my data file record reflects the true species identity any of the *Aspilota* species.

I am not sure what the *Aspilota* sp. (Table 2, No. 1a) and the *Aspilota* sp. (Table 2, No. 1c) records refer to. They may mean *Aspilota* but, if that is so, I doubt the validity of the record. I also question the records for *Aspilota* sp. (Table 2, No. 1a, 1c) and *Aspilota* sp. (Table 2, No. 1).



In general there seems to be three families of plants attacked, the Euphorbiaceae, the Sphenocleaceae, the Portulacaceae. The Euphorbiaceae are infected by *Heliothrips obliqua* (Gill.) (On *Myrica caroliniana* L. and *P. angustifolia* L.) and *Heliothrips peruviana* (Guer.) (On *P. latifolia* L.). The Sphenocleaceae are infected by *Heliothrips peruviana* Gill. (*Sphenocleus albus* Art. and *P. peruviana* DeCais.) and *P. obliqua* (Fisher 1912). The Portulacaceae are infected by *Acanthosoma obscurum* (Gill.) (*Portulaca oleracea* L. and *Portulaca ananensis* (Pers.) Solms). This supports Todd's (pers. comm.) contention that possibly only three species are involved.

A fourth family, the Araceae, is strongly implicated within the host range of this family. Geyer's (1882) record (Table 2, No. 1a) of *Acanthosoma obliqua* (Gill.) from stem damage (*Spatholobus lundbeckianus* A. Schottianus + *anacardium* Willd. & St. John, see Ross 1955) seems to be well founded. Hattala's (1882) citation of *Sphenocleus carolinensis* L. (Table 2, No. 1c) probably refers to Geyer's paper. Halsek's (1924) record of *Acanthosoma obscurum* Gill. from *Salicornia* (*Salicornia vermiculata* L. = *Salicornia vermiculata* G.) Schott. (Table 2, No. 4a) also seems well-founded. These represent two instances of the infestation of two different species of the Araceae from two widely separated regions (British Columbia, Geyer 1882 and Florida, Halsek 1924) by apparently two species of the *Heliothrips* complex. Williams (1955) indicates that there is a close affinity between the Liliaceae (Portulacaceae), Araceae, and Euphorbiaceae and they all are represented along a line of evolution in common with the Sphenocleaceae.

Fisher (1912) stated that *Acanthosoma obliqua* has been reported from corn. He did not cite any references to these reports, however, and I have not been able to substantiate this claim. Because crop plants such

as distinct and new have been indicated in the host range of this group of insects a great deal of study of host specificity is warranted and the taxonomic status of the group needs clarification. I do not doubt these records but I am dubious of the placement of species identified from these plants. On several occasions I have tested larvae of *Araneus doxus* (Wlk.) on both *Androsace foliolosa* (Schott) and *Androsace* sp. and found that they did not feed upon them. Further studies are severely needed to verify these host records.

#### Biology and Life History of *Araneus doxus* Wlk. and Related Species.

The early literature on the biology of these species is sparse and covers primarily as notes of correspondence in various journals. The first reference I have been able to find is that of Northampton (1881). He described the larva of *Araneus obliquus* (G. & B.) and noted that it was found "under the bark of a dead maple about three feet from the ground, where it had made the larva its usual dwelling in the dust." He reared the adult and found that the pupal duration was about 21 days (April 21 - May 14).

Emerton (1881) described the larva and aquatic habits of *Araneus melanopus* Wlt. He was the first to take note of the large dorsally situated pair of spiracles on the 4th abdominal segment which are characteristic of the larvae of this group.

Wieg (1883a, b) described the eggs of *Araneus obliquus* G. & B. (designated *Araneus*) as being laid in "thinly or broadly spread or plane-concave masses enveloped in hair, and a cream-colored mucous secretion, when combined look much like some silk on the spindle, and on the surface like the glass envelopes of *Oryza leucostigma*." He also noted the

large dorsally oriented first pair of setae). He stated that there were two small broods, the second of which hibernated in stacks or rows near the water.

Buffett (1984a, b), however, felt sure that in New York this species was always brooded and pupated in hay. He also noted that they overwinter in the soil or old wood.

Fraser (1984a, b), in reply to Buffett's comments, stated that there could be no doubt as to the oligoneuric (=adults brooded) nature of *A. vitripennis* at distribution 1b, c, f.

Conant (1986) referred to the habits of *A. argens* (mis spelled *argens*) that inhabit the leaves of road irises. He distinguished these from truly aquatic larvae in that they "are obliged to come to the surface" for air.

Brooks (1986) described the eggs, larvae, and pupa of *A. vitripennis* (B. & B.). He noted a developmental period of about 15 days for the eggs which were laid in cattails between the long leaves. He found the larval period to be 161 days and the pupal period to be 16 days making a total egg to adult span of 196 days.

Brooks (1986) also stated that the larvae resound to the top of the mud to its water level stage and form its pupa there. This marked a series of correspondence to the Canadian *A. latreillei*. Buffett (1986a) stated that this was not its hibernable habit in nature and he had found the pupa beneath the bark of a decaying stump some distance away from where the cattails grew. Brooks (1986) replied that this may not be hibernable but that the majority of them reside in the mud. He cited a friend of his who had found the pupa in a stump but indicated that the larvae had been feeding there and wondered if that wasn't true in Buffett's



case. Buffett (1888) replied that there was no evidence that the larvae had fed in the slumps and that all of the larvae and pupae they collected were in similar situations, not subjected to any feeding, looked in the type slumps for most of a hour.

Aglicotti (1893) referred back to the correspondence between Riley and himself in 1892 and had decided that they were both right in that *A. caliginea* ♀ & ♂ produced two broods in Washington and one in New York. He also presented evidence conflicting Buffett's conclusion that they overwinter in slumps as larvae. Brown (1898) later sent sections of type slumps to Buffett with numerous larvae and two pupae. Buffett (1899) subsequently reared a pair of the adults from this material. Brown (1899) felt that Aglicotti and Marshall were mistaken in their assertion that the larvae overwinter in slumps because the specimens he sent to Buffett were collected in the winter before the water in certain reefs and some were even under ice. He also disagreed with Riley over the clustering mode of oviposition. He noted that he had always found eggs laid singly and felt that if it were otherwise it would be impossible for several larvae to live in one reef. Johnston (1911) agreed with Brown as he had found clustered larvae and pupae in certain in the water in Ontario. He noted, however, that he had also found them on shores in old mud. He proposed that these on shores were merely wanderers. Bartmeiller (1919) described the winter larval of this species and indicated that he had found full grown specimens under decaying stumps. He later (Bartmeiller 1922) described the larva again under the name of *Aspilota caliginea* [sic].

Benson (1914) repeated Comstock's (1892) description of the larva of *Aspilota caliginea* Grt. under the name of *Aspilota caliginea* [sic].

Wick [1914] described the habits of *Agropyron triflorum* (Gussak.) He described two feeding periods, first being the leaf-feeding period in which the young larvae enter the leaves of *Agropyron monspeliense* (Hayden variegated). The second stage is the petiole period which occurs after the larvae locate the joints or the leaf-petiole junction and forms a large burrow in the petiole. He also experimented with other host plants. He found that in a starvation situation they would feed on white water lily, *Najas* (a spongy) plants but when given a choice preferred the yellow water lily, *Potamogeton zosterifolius* and *Agrostis* sp. were never attacked. He also discussed respiration, locomotion, and the seasonal changes of this species.

Samuel [1915] noted that cattail plants bearing spikes were not infested with *Agropyron*.

Johnson [1921] published a detailed account of the insects associated with *Agropyron*. Included within this was an excellent study on the biology of *Agropyron* (Wick). He found, in New York that there was only one generation per year and that the full grown larvae overwinter in the burrow in the plant. He described the mode of oviposition to be in masses, similar to the description given by Wick [1914, p. 1]. He found that each mass contained 25-40 eggs and each female produces an 275 eggs mating about 4 masses per female possible. Upon emergence the first instar larvae enter the leaf directly from the egg cluster. They feed within the longitudinal U-shaped partitions within the leaf sheath downward. At the second molt they apparently become too large to feed within these partitions and emerge from the leaves and seek shelter behind the sheath of one of the outer leaves. They ultimately disperse, each to feed its own plant, and become solitary burrowers in the stem and rhizome. These, then, exhibit two phases similar to those of Wick [1914]

although these should probably be called the leaf mining phase and the mine phase (rather than the petiole phase). He noted that the length of the pupal period averaged 17.8 days and described the egg, first instar larva, full grown larva, pupa, and adult (from culture).

Robertson-Effler (1921) published some observations on the biology of *Acleria guayanaensis* Wlk. and *A. malayana* Grt. Her information did not differ much from that of Welch (1914). She described the larvae of each and indicated that they did not appear to be much different. She described the egg masses and indicated that those of *A. guayanaensis* were deposited in flat rows of about 30 eggs each. She noted that some of the eggs were covered with silvery white threads. The masses of *A. malayana* were similar to those of *A. guayanaensis*. She found that *A. guayanaensis* pupated in the petiole, in soil, or in wood. When in the petiole the pupa of *A. malayana* was at the top of the burrow while those of *A. guayanaensis* were lower down. She also found that *A. guayanaensis* would feed of pickaninnet (*Proteinaria cordata*) in captivity.

Needham et al. (1935) repeated the observations of Claassen (1911) on *Arauca* (= *Acleria*) *obliqua* (Grt.) and of Welch (1914) on *Acleria malayana* Grt.

Constock and Osborn (1949) described the full grown larva and pupa of *Arauca guayanaensis* (Sp.). There is no distinction between this description and previous authors' descriptions of these stages of *Acleria obliqua* (Grt.)

Gray (1948) described the habits of *Arauca* (= *Acleria*) *obliqua* attacking black cabbage (*Spontanea histiodesmacea*) on Yacouet Island, B.C. He also indicated that they overwintered under loose bark on fallen logs.

Crypte (1866) provided a key to the larvae of the Amphigyrinae. The simplest separating device used the large sub-dorsal spiracles as the 5th abdominal segment as a key character. He also described the larva of *Anura obliqua* (Gyll.).

Reger and Oliver published two papers (1886a, b) on *Anura domus* Gyll. Their first paper was on the rearing of this insect to control waterbugs etc.. Their second paper was on the life history of *A. domus*. They provided country descriptions of the immature stages and tabulated the developmental times of the various stages. Both of their data, however, is from larvae reared on artificial diets which makes their results subject to question. These two papers will be further discussed later in this dissertation.

Lawton (1944) found that in Indiana there were two complete generations per year of *Helorus perpendicularis* Gyll. (= *A. subcapitata* Gyll.). He found that the first generation (spring) pupated within the petioles of *Asplen adnigrum*. The second generation (fall) larvae seem to thrive and overwinter as larvae under the bark of trees, in rotting wood, or in leaf litter. The eggs hatch in 4 days and there are 4 to 7 instars.

#### Parasites, Predators, and Diseases.

The first record of natural enemies which attack this group of insects was that of Balch (1914) for *Helorus melanopygus* Gyll. He noted that coccinellids ate the larvae when they were molting on the surface. He also observed water beetles (*Hydroporus* sp.) attacking the larvae when they were on the surface of the leaves.

Lawson (1921) found *Stenomacrus signatus* Loew. (Diptera: Cecidomyiidae) parasitizing the larvae of *Anura obliqua* (Gyll.). Robertson-Keller (1944)

found puparia of *Epilimnobia* associated with the larvae of *Helium periporoides* Wlk. Both of these items are probably synonyms of *Epilimnobia rubens* [Fenn] (Stannard et al. 1965).

Constock (1940) made note of the fact that he found no parasites associated with *Helium periporoides* Spur in California.

In the Thompson catalogue (1890) two parasites are listed from *Helium oblique* [Wlk.]. The first is *Microgaster areolaris* Mgr. which may be a misidentification of *Epilimnobia rubens* [Fenn.]. The second is *Phaenocarpa* P. [Hymenoptera] which is an ichneumonid. I question the validity of this latter record, however, because the name is listed throughout Europe, Japan, and Guam. As far as I have been able to ascertain the *Helium-Helium* group is strictly the World.

Paper and Stinner (1938) listed several parasites and predators of *Helium dross* Wlk. They identified *Epilimnobia rubens* (Fenn.) from the larvae, *Ichneumon* n. sp. and *Epilimnobia viridescens* [Rufolt] (Hymenoptera: Pteromalidae) from the pupae, *Ichneumon areolaris* Riley (Hymenoptera: Epilimnobia) and *Microgaster* sp. (Hymenoptera: Epilimnobia) from the eggs. They also found *Colletes* sp. from the larvae (Coleoptera: Curculionidae) preying on the eggs and young larvae, and *Phaenocarpa pulchella* (Rufolt) (Orthoptera: Gryllidae) and *Ichneumon pulchellus* Say (Coleoptera: Carabidae) preying on the larvae.

Larson (1954) indicated that the eggs of first and second generations of *Helium periporoides* Wlk. are also parasitized by *Ichneumon areolaris* Riley and the second generation larval populations are parasitized by an ichneumonid and have a polydromous view.

## CHAPTER I

### THE RELATIONSHIP BETWEEN THE PHENOLOGY AND PRODUCTIVITY OF AUTOMNACTS AND VARIOUS PHYSICAL AND ECOLOGICAL FACTORS

#### Introduction

To evaluate the effects of insects for the biological control of weeds, a basic understanding of the ecology of the plant is essential. In realization of this, the Canada Weed Committee has instituted a series on the biology of Canadian weeds (Gowers and Halligan 1972). This is an attempt to put together all the available knowledge on the biology of Canadian weeds that can be used to meet control efforts. Within this framework the phenology of the plant (seasonal variations), and the response of the plant to limiting factors and damage by indigenous insects is of special interest for the evaluation of biological control attempts. Deletion of these considerations could result in the misinterpretation of pertinent data. For example, seasonal seasonal declines in the plant population could mistakenly be attributed to insect release when the insects are also seasonal. If patterns of seasonal variation of the plant are not known, then, releases of insects may be more effective when correlated with critical periods in the annual cycle of the plant. Judgements for the timing of insect releases can be made only on the basis of what is known about the plant.

Limiting factors can be defined as the necessary components of the organism's environment which are least available and thereby control the life processes of the population. Lillie (1940) stated that a process is limited by the scarcity of a single component present in almost amounts relative to its optimal demands. Smith (1960) felt that biological processes required a certain critical level of a limiting

factor to begin, assumed as optimum at a certain level, and declining as levels of the limiting factor exceeded maximum tolerable levels. This is parallel to Shelford's (1913) 'Law of Tolerance' where he essentially states that the failure of an organism may be due to an excess or deficiency of any one factor which may approach the maximum or minimum limits of tolerance of the organism for that factor. For an aquatic plant, such as waterhyacinth, these limiting factors include temperature, light, water, dissolved or available nutrients, space, etc.

Phytophagous insects probably cause a threshold type response in the plants whereby the plant can sustain certain levels of damage without obvious deterioration until maximum tolerable limits are exceeded. As insect damage exceeds these threshold levels a rapid decline in the population or standing crop may be evident. Levels of insect damage below this threshold may cause various plant responses. When the population is at steady state (the stable maximum level restricted by the level of a limiting factor) insects may disrupt this stability causing the plant population or standing crop to fall below the carrying capacity of the system. This may have the effect of reducing intraspecific competition in the plant population. In this case the limiting factors would become increasingly more available and production may indirectly be stimulated. Insect yield may be increased under the insect concentration where the insects prevent saturation of the population by increasing the rate of turnover.

This study was designed to measure the effects of various environmental factors as well as the effects of a natural buildup of an indigenous insect population (brown down) in a stand of waterhyacinth. The parameters considered can be grouped into climatological coefficients (temperature and solar radiation), limnological coefficients (nutrients,

water quality and water level), intraspecific conditions (plant density, canopy effects, available space, etc.), and biotic stress (insect damage). These will be evaluated with possible interactions between them considered.

These concepts, possible interactions and all factors which control the plant must be considered and investigated. Attempts to evaluate the attack of an insect by studying only the insect or with only a superficial knowledge of the target plant are subject to erroneous conclusions and misinterpretation; not only must the plant and the insect be studied but the insect-plant interrelationships must be established. This field has received increasing attention lately and may provide a basis for future (integrated) control efforts.



## Methods And Materials

### General Botany/Leaf Productivity

Representative of two distinct morphological types from the "open" side of the wetlands on Lake Abasco were selected for in situ metabolic studies. Large plants, approximately 80 cm tall, with elongate petioles were measured for  $\text{CO}_2$  uptake on 11-12 August 1972. Small plants (<30 cm with bulbous petioles) were measured on 11-12 August 1973. A section of the wet approximately  $0.5 \text{ m}^2$  of each type was placed under a chamber constructed of a PVC pipe frame covered with clear polyethylene. The base of the chamber was 70 cm x 70 cm (or  $0.5 \text{ m}^2$ ).

Air was passed through the chamber with a blower and duct system. The duct entered the chamber at the base on one side. Air was supplied to the blower intake through a tube opening approximately 3 m above the water surface so the  $\text{CO}_2$  concentration would not be influenced by the plants surrounding the chamber. The rate of air flow was determined with a Hastings hot wire anemometer. The air was discharged from the chamber through a duct located on top.

Carbon dioxide concentrations were monitored at the chamber air intake duct end at the exhaust end. The air at each location was collected through tubes which extended to a Beckman infra-red  $\text{CO}_2$  gas analyzer. Air flow was also measured at the intake and exhaust. This enabled the determination of the ppm  $\text{CO}_2$ /unit of air flow entering and leaving the chamber. The differential is the amount of  $\text{CO}_2$  produced or consumed within the chamber.

The  $\text{CO}_2$  analyzer readings had to be calibrated against a standard

to convert from a scale reading to ppm  $\text{O}_2$ . The scale reading is based on a comparison of two gases. Three pairs of gases were compared through the analyser: ambient air vs. ambient air (air entering the chamber) was compared to determine a zero point. The second comparison was chamber exhaust vs. ambient air. This difference represented the  $\text{O}_2$  gradient through the chamber and was expressed as recorder scale division. The value of a scale division (sd) is determined according to the level of  $\text{O}_2$  in the ambient air by the equation  $\text{ppm} = \text{sd}^{100}$  where  $x$  is the  $\text{O}_2$  concentration of the ambient air. The ambient air  $\text{O}_2$  concentration was determined by a third comparison. In this case a standard was used of a known concentration. The standard was 300 ppm bottled gas and was compared against the ambient air. The  $\text{O}_2$  concentration in the ambient air was determined by the equation  $\text{ppm} = \text{sd}^2 + 3\text{sd} + x$  where  $x$  is the recorder reading. This involves lowering the amplification of the analyser signal by changing from "range 3" to "range 1". The range 1 equation is calculated by running the standard 300 ppm gas through the reference side of the analyser and running other gases of known concentration through the sample side. The value of the sample gas is correlated with the recorder reading using the parabolic regression. Range 3 is calibrated using various known  $\text{O}_2$  concentrations against a closed system operated with flow and pressure isolated checked. The closed system is injected with known quantities of pure  $\text{O}_2$ . An exponential regression is fitted for the ppm/sd against ppm  $\text{O}_2$  of the various reference gases (ambient air is this case).

The volumetric  $\text{O}_2$  concentration gradient (ppm  $\text{O}_2$ ) is converted a gravimetric measurement (g  $\text{O}_2/\text{m}^2$ ) using the gas constant (8.14428 gm  $\text{O}_2/\text{m}^2$

area per  $\text{O}_2$ ), when multiplied by the flow rate this expression yields the rate of carbon metabolism ( $g \text{ CO}_2/g$ ) within the cluster. A more detailed explanation of this system is given by Carter et al. (1970).

Carbon metabolism for each type of plant was measured for 24 hrs. Interpretation of the resultant production curves plotted both gross primary productivity and respiration. Respiration was assumed to be constant both day and night and was determined as the average nighttime value. Net production consisted of that portion of the curve above the compensative point (where  $P_n = 0$  and  $P_g = 0$ ); solar radiation was measured with a liethermometer Co. 25-in. pyrhaeliograph in the 0.25-2.5  $\mu$ m range. Air temperature was recorded using a Dallas Springs Instrument thermistor apparatus.

Following the metabolic measurements the plants were harvested to obtain a biomass estimate. The total sample was divided into leaves, petioles, roots ( $=$  roots + rhizomes + stolons) and tubers and the various plant parts were weighed while fresh. A similarly divided subsample was taken and weighed before and after drying. From this subsample a wet to dry conversion factor was obtained so that the dry weight for each plant part and the total sample could be obtained. A subsample of the leaves (pseudostems) and petioles was pressed in a plant press and dried. The outlines of the dried leaves were traced on paper and the area measured with a planimeter. This determined a leaf area per gram of dried leaf conversion factor and the leaf area of the total sample was calculated from this. A similar procedure was employed with the petioles. From this the leaf area index (LAI) was determined which, in this case, is the total leaf area (leaves + petioles) per square meter as determined from only one side of the leaf.

### Annual Cycles and Insect Damage

Estimates of various plant characteristics, of the *Anaxyrus* density population, and of plant damage by *A. axyrus* were taken on a weekly basis from May 1974 to 30 April 1976. Sampling was done on a plot system using a rubber ring enclosing an inside area of 8.24 m<sup>2</sup>. The samples were taken each week in a pseudo-random manner. I have not been able to devise a satisfactory system of prepositing a previously randomly selected point as a set of waterhyacinths and then finding that point while trying to swimmer through the dense stand of plants. To eliminate the additional variables of seasonal plant species competition changes arising for selection and different waterhyacinth growth characteristics only the control area of the lake was studied. The area in which samples were taken was defined by the culvert on the west side and extended 25 m to the north and 25 m to the south of the control point on the culvert. The eastern boundary was established by a well row of timber 50-60 m from the culvert that extended into the lake from the north shore. The study area, then, was 1000-2000 m<sup>2</sup> in the control area or less homogeneous region of the waterhyacinth mat on the north side of the culvert. Sampling points were selected by throwing the ring in a high arc. After it fell into the mat it was reached using two (one aluminum stillets (2 m x 8.4 m), one placed in front of the other staggered slightly. This allowed us to move (after some effort) over the mat on the water surface. Once the ring was reached the stillets were used as platforms for sampling and recording data.

The ring was manipulated down over the waterhyacinths until it was on the water surface. This involved making six or seven decisions as to

whole plants were inside and which plants were outside the sample. If the crown was in the ring the whole plant was considered in. This was still difficult to determine when the crown straddled the edge. The placement of these plants was left up to the discretion of the sampler. This border effect was probably the largest within sample source of error in the plot sampling.

Since the ring was placed each plant was identified and numbered. An effort was considered a separate plant only if the root system was developed. Measurements taken were the height of the plant, based on the distance from the tip of the longest leaf to the point where it attached to the rhizome, and the number of leaves per plant. Leaves were counted only if half or more of the petiole/node was above and unfolded. The number of plants in each plot was tallied to establish plant density. Each plant was carefully detached and damage by *A. nemus* above noted. Damage was distinguished according to the degree of severity. Leaf damage was classified as to internal feeding or petiole bore. Rhizome damage was classified as tip damage, rhizome bore, or rhizome fragmented. If a larva or pupa was found it was placed in a pill vial, given an identifying number and returned to the laboratory. The larval data will be discussed in a separate section of this dissertation. One sample required 3-4 man-hours. Three samples were taken each week.

Leaf area estimates were also taken weekly but in a different way. Ten plants were randomly selected along the cobble for this measurement. The randomization procedure consisted of scattering the supporting gillnets of the catwalks within the study area. Ten gillnets were selected from generated random numbers. At each selected gilling a single plant was

picked. This required a second randomization. One person involved in the process held a sorted generated random number between 1 and 10. A second person drew up to ten plants out of the water. When the  $a^{th}$  plant (where  $a$  = the random number) was pulled out the first person notified the second and the plant was placed in a plastic bag and returned to the laboratory.

Before measuring the leaf area the petioles and leaf blades (pseudoblades) were separated. The petioles were rolled out with a rolling pin. This was necessary to compensate for the cylindrical shape of the petiole. The outline was then traced on a piece of drawing paper and measured with a planimeter. The leaf blades were pressed in a plant press and dried. They were then traced and measured the same way. I found that drying the leaves caused considerable shrinkage and a dry-fresh conversion factor had to be employed. The formula for this conversion was

$$\text{leaf area (fresh)} = 1.40 \times \text{leaf area (dry)}$$

The conversion factor was determined by measuring one sample (51 leaves) before and after drying. Each week figures for the average leaf (pseudoblade) area, average petiole area, and average total (pseudoblade + petiole) leaf area were derived. These figures were multiplied by the number of leaves per square meter from the plant samples to obtain the leaf or petiole area index. This figure represents the leaf or petiole surface area (considering only one side) per unit of substrate area ( $\text{m}^2/\text{m}^2$ ).

Water samples were taken along the collector at the mid-pool. The water was collected a few centimeters below the surface at the level of the waterpump/belt route. This level should best reflect the conditions the plants were being subjected to. The sampling station was in the downstream 1/3 of the study area so the tests would reflect changes

nutrient levels. Two samples were collected each week; one sample was analysed using a Bach 94-D portable test kit for total alkalinity (carbonate + bicarbonate), total alkalies + nitrates, pH, total phosphates, and sulfate and a Bach micro-flow test kit (model 10-10-4) for iron. The second sample was taken to the University of Florida Gulf Laboratory where it was analysed for conductivity, magnesium, and potassium.

The methods applied to the water samples are as follows:

- Alkalinity (total) - Titration of Free Green Green - Methyl Red indicator with 0.02N sulfuric acid - 10 ml sample
- Conductivity - Platinum electrodes - ohmmeter
- Iron - 1, 10 - Phenanthroline Method - 25 ml sample
- Magnesium - Allen's absorption spectrophotometer
- Nitrates and Nitrites (total) - Cadmium reduction method - 25 ml sample.
- pH - Colorimetric reading with a wide range indicator.
- Phosphates (total) - Colorimetric method - 25 ml sample
- Potassium - Flame emission spectrophotometer
- Sulfate - Turbidimetric method.

The procedures employed in the Bach Test kit are more for convenience and effect reading and are not as accurate as other techniques. For my purposes the loss in accuracy is outweighed by simplicity of the procedures. These procedures are probably accurate enough to indicate temporal differences but are probably not extremely definitive.

Room and surface air and water temperatures were taken at the same location as the water samples. Two Taylor (No. 5440) maximum-minimum self registering thermometers were mounted on a C-shaped aluminum

1968). The water temperature thermometer was placed vertically on the bottom of the block. The air temperature thermometer was placed vertically in the narrow side. The block was mounted on a meter which slid over a piece of pipe which extended into the lake bottom. This allowed the thermometer to move up or down as the water level changed. The bulb of the underwater thermometer was about 4 cm below the surface and measured the conditions the submerged plant portions were subjected to. The air thermometer bulb was about 30 cm above the water surface and measured conditions under the leaf canopy. The narrow side of the block was oriented towards the north so as to avoid direct exposure to the sun. The overhang on the block also helped prevent this.

Water level was measured at the northeast corner of the study area from a depth gauge established there previously by other investigators. Solar radiation data was obtained from Dr. E.-B. Parker of the solar energy laboratory at the University of Florida.



### Site Description

Lake Alice is located in the southeast corner of the University of Florida campus in Gainesville, Flakata Co., Florida (Topographic designation: Gainesville test quadrangle, T10N, R10E, 00N, 01W, 00A). The lake was once a shallow pond by a small stream but during off the wet out in the late 1940's and later the addition of effluents from the campus sewage treatment plant and the testing plant resulted in the present configuration (see Figure 1). The lake area is approximately 25 ha and is divided into a marsh sheltered by waterhyacinths and an open water-land by the University as open water. The marsh at the west end comprises approximately 60% (15 ha) of the lake surface and is separated from the open lake by a natural and fence constructed to retain the waterhyacinths. The depth of the marsh is generally less than 2 meters (Cason 1973). The "open" water end of the lake covers about 12 ha and is also generally less than 2 meters in depth with a few areas of about 5 meters, probably the original condition (Orbach 1981). The general flow of the lake is from the sewage plant and testing plant effluent at the western end through the marsh to the open lake at the eastern end where it discharges through two weirs into the Florida buffer.

The lake is situated on local limestone which is dolomitic by a karst topography. Subsurface channels, fractures, and caverns are typical of this type of topography and are common in this area. Because of the silt that has accumulated on the bottom, however, the lake basin is maintained above the local water table (Cason 1973). The lake level is generally between 64 and 70 feet above mean sea level. Figure 2 indicates the lake level at the outfalls for the period of this study.

Figure 1

An aerial view of Lake Atitlan in the Volcans of Maricao shows the lake's position relative to the surrounding mountains. The lake is located in the center of the volcanic range, with the lake's surface area of 100 km<sup>2</sup>.



As mentioned previously Lake Alice receives effluent from the campus sewage treatment facility and cooling water from the heating plant. The nutrient enriched water from the former and the lake water from the latter have probably contributed significantly to the eutrophication of Lake Alice. Other sources include overflow from Rose Pond, also located on the university campus; runoff from the local watershed, and direct rainfall. Discharge of desigilants through the walls mentioned earlier-water loss also occurs through surface evaporation and evapotranspiration. Mitsch (1975) estimated the hydrological budget for the lake in terms of flows and storage (see Table 3). The water storage at a stage of 66 feet above mean sea level is estimated to be  $284 \times 10^6$  m<sup>3</sup>. Water retention is the due to the high input-volume ratio. Dracup et al. (1984) suggests that this may have a flushing effect causing low phytoplankton populations noted in the lake.

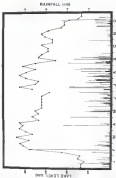
Discharge through the walls is regulated by valves and is frequently opened by campus personnel. The water level is often raised to facilitate mechanical removal of the waterhyacinths. During the hydrologic season the water level is dropped to prevent flooding. Fluctuations are also caused when the discharge screens over the walls become clogged with debris. Water level appears to be correlated with seasonal precipitation patterns (Fig. 4) except for the months of December and January. During this time an oil spill occurred in the canal from the heating plant and sewage treatment facility. Flows from these two sources were interrupted so the spill could be cleaned up. This resulted in a sharp drop in the lake level. Normal flow was restored the first part of February and a sharp increase in the lake level followed.

Table 3: Hydrological budget for Lake Alton (March - September 1951) (From Hirsch 1976)

Source	Input*	Output*
Drainage Flow	30.5	---
Runoff from Flow	48.5	---
Base Emission	5.5	---
Street Sewerfall	0.5 - 2.0	---
Runoff	4.1 - 21.0	---
Transpiration	---	1.5 - 3.1
Evaporation	---	0.5 - 0.6
Discharge	---	54.0 - 56.5
TOTAL	49.5 - 55.5	46.2 - 49.8

\*Flow in  $10^3$  m<sup>3</sup>/day

Figure 2. Water (mm) taken at weekly intervals and precipitation at Lake Arrow from July 1971 through June 1972.



### Analysis

Regression analysis was performed on the actual data in an attempt to account for observed variation in the plant characteristics in terms of the various environmental parameters. A stepwise regression procedure (SAS STEPWISE) was first employed to determine which linear combination of independent variables would provide the best fit for the actual data. The dependent variables analyzed were standing crop, plant height, plant density, leaf density, average leaves per plant, and leaf area index. Each was regressed against water radiation, minimum air temperature, maximum air temperature, minimum water temperature, maximum water temperature,  $\Sigma$  relative degree by degree above,  $\Sigma$  leaf degree by  $\Sigma$  above, all other water quality parameters, and water level. Three procedures were employed to determine the best regression equation. These were the forward selection procedure, the backward elimination procedure, and the stepwise procedure. All gave linear models in different ways (see SAS manual, 1972 for further explanation). Each provides an analysis of variance, regression coefficients and statistics of fit for the model. In all cases the stepwise procedure provided the most significant fits to the data.

Two additional variables were entered which were derived from other variables. Since it was assumed that the amount of light intercepted by the plants would be roughly proportional to the degree of leaf shading the water radiation variable was divided by the leaf area index to form a new variable. This was entered into the analysis in place of incident water radiation but it failed to increase the significance of any of the linear combinations (i.e., incident water radiation was just as good or better). It was also speculated that available space may contribute to



growth. A variable for space was forced which was merely the inverse of the leaf area index and added to the data. In many cases this did increase the significance of the regression equations--upon further consideration. It became apparent that the inclusion of this variable was not valid since it was derived from a dependent variable. Available space would obviously be greater when the standing crop is at a minimum and would certainly be inversely correlated with it. An increase in space may very well increase the rate of growth but rates were not being analyzed. The dependent variables represent the state of each parameter which is regressed against the corresponding states of the independent variables. For these reasons space and shading were excluded in the final analysis.

Once the model for the best fit was derived it was entered into a regression program (SAS REG Procedure). This program provided the same analysis as the stepwise procedure but in addition it predicted values for the dependent variables based on the multivariate model with each set of independent variables.

The linear model assumes orthogonality between independent variables. Since many of the parameters were inter-related (i.e., sun and air temperatures, disease damage and leaf damage, etc.) the assumption of orthogonality is violated. In evaluating a model the procedure may select the parameter which best reduces variability and important correlated variables may be lost. For this reason a correlation procedure (SAS CORR Procedure) was employed to determine which variables were significantly correlated. As a result, if a factor is found to significantly contribute to variation in the dependent variable it can be cross checked in the correlation matrix to determine what other variables may be working with it. The dependent variables were also checked against one another for significant correlations using the same procedure.

A major weakness in the use of a multivariate linear model in this type of study is that it assumes independence between independent variables. In actuality probably very few of the variables are completely independent. For example sunlight and nutrient levels are both assumed to be linearly related to the state of the variable for standing crop. It is further assumed that each contributes independently and in an additive fashion. This is not true, however, as variables such as nutrient levels and solar radiation interact multiplicatively and the effects of one are limited by the value of the other (see R. T. Odum 1984). This interaction may be linear, exponential, or logarithmic depending upon whether or not either is present in limiting quantities. The linear model does not account for these complex relationships and should not be considered as a basis for making generalizations about interrelationships in the system. I feel, however, that this type of analysis can provide an indication of which variables are important in accounting for variation but it cannot be interpreted as a mathematical expression of the functions of these variables (i.e., the coefficients in the model have no real meaning).

## Results

### Water Quality

Lake Alice has been variously classified as eutrophic, highly eutrophic, and mesotrophic (Brazneris 1981, Brazneris *et al.* 1988). Brazneris *et al.* (1988) reported that lake nutrient levels do not reflect the nutrient enrichment source inputs that feeds the lake. They postulated that this was due to ability of the waterhyacinth to absorb these nutrients. This was corroborated by Hirsch (1975) who found that various nutrient concentrations decline in the direction of flow across the marsh. Brazneris *et al.* (1988) also found that phytoplankton counts were extremely low and suggested that this may be the result of light blockage by the waterhyacinth as well as a flushing effect of the large volume of cooling water from the heating plant. Table 4 lists various water quality ranges for the lake from Hirsch (1975), Brazneris *et al.* (1988) and from this study. The former two investigators followed standard procedures as established by the American Public Health Association (1945). I did not have the facilities to follow these procedures and used a water chemistry test kit for pH, nitrogen, phosphorus, sulfates, iron, and alkalinity. The samples were further analyzed for conductivity, potassium, and magnesium by the University of Florida Salt Laboratory. In spite of this divergence in technique and methodology the values from my study compare favorably with those from the other studies. However, my values are not definitive and are only general indices of the parameters measured.

Figures 2 - 7 illustrate seasonal changes in the water quality parameters measured. Because of the many factors affecting nutrient loads it is difficult to explain the variations observed. The amount of waste

Table 4. A comparison of water quality measurements from Lake Okeechobee, Collier Co., Florida with previous reports.<sup>1</sup>

Source of Data	measured as at (1984) <sup>2</sup>	measured (1991) <sup>3</sup>	this study <sup>4</sup>
Time Period	Apr. 1989	Jan. - Sept. 1991	July 1989-Sept. 1991
Water Sampled	Composite of 3 Stations	North discharge	North discharge
by Conductance	122	279 - 409	484-521 (441-561)
alkalinity	126	100 - 360	129-360 (219-519)
pH	7.8	7.0 - 8.2	7.33 (6.95-7.71)
NO <sub>3</sub> (N)	0.28	0.052 - 0.188	---
NO <sub>2</sub> (N)	0	0.008 - 0.028	---
NO <sub>3</sub> (N)	---	0.26 - 0.62	---
NO <sub>3</sub> + NO <sub>2</sub>	---	---	0.33 (0.18-0.48)
nitrite (P)	0.07	0.10 - 1.32	---
nitrate (P)	0.08	0.00 - 2.16	1.32 (0.40-2.24)
Chloride	16.7	---	---
Sulfate	16.8	1.1 - 19	---
Calcium	71	18 - 36	---
Iron	0.01	---	0.263 (0.002-0.523)
Ammonia	---	0.5 - 3.3	2.43 (1.3-3.6)
Sulfate	---	---	852.8 (426-1318)
Phosphate	---	0.5 - 14.6	81.26 (1.5-162)

<sup>1</sup> Florida Department of

<sup>2</sup> Data based on monthly averages

<sup>3</sup> Mean 2 standard deviations (SD) of 171 samples for the time period

<sup>4</sup> Data in Sept. except for ammonia (ammonia), pH (pH values), and alkalinity (ammonia + NO<sub>3</sub> in Florida and alkalinity and as NO<sub>3</sub> + NO<sub>2</sub> in this study)

treated varies with the number of students present at the university at different times of the year, varied from the sewage treatment plant water, the amount of water (doses, the diluting effect) from the backing plant water, rainfall varies as does runoff from more fertilized farmland. All of these factors affect nutrient concentrations. Since the samples were taken from the study area, however, they should reflect the relative conditions the plants were growing in at the time. The reasons for differences in the nutrient levels are not important but the differences themselves are.

Alkalinity (Fig. 1) generally ranged from 140 to 210  $\text{mg/l}$ . Concentrations were fairly constant. The greatest fluctuations occurred in December when a sharp drop was apparent and in January when an equally sharp increase occurred. The concentration at the end of the study (11 April 1975) was somewhat higher than that at the beginning (20 June 1974). Alkalinity is a measure of the buffering capacity of the lake and is indication of eutrophication.

Conductivity (Fig. 2) ranged from 200-600  $\mu\text{mhos/cm}$  and is a measure of the electrical conductance of the water resulting from ionic salt concentrations. The conductivity values fluctuated greatly throughout the year. In general periods of low conductivity seemed to correspond to periods of frequent rainfall. This is presumably due to a dilution of the soluble salts present relative to the water storage of the lake.

Iron (Fig. 3) was measured because I have observed in greenhouse cultures that waterhyacinths grow much better in nutrient solutions high in iron concentrations. Further, it appeared that the iron in the solution was rapidly absorbed by the plants. Iron is a constituent of cytochromes and as such is an essential micronutrient for plant growth concentrations in this lake were less than 0.10  $\text{mg/l}$  most of the year.

Figure 2. Total variance and intercorrelation illustrating and conductivity of other sampling sites from Lake Atitlan from July 1981 through June 1982. The three eigenvalues (boxed) mirror results.

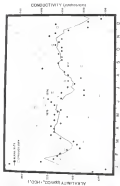


Figure 4: Reproductive and total iron from Lake Michigan samples, 1966-1970. The data show a decrease in iron concentrations in April. The lines represent 5-year moving averages.





but a curious sharp rise occurred in April where the maximum concentration of 8-40  $\mu\text{g/l}$  occurred. Concentrations dropped in May and returned to initial levels in June.

Nitrogen is an important structural component of the chlorophyll molecule and is also used by plants in the metabolism of carbohydrates. It is therefore also an essential element for plant growth. Nitrogen levels remained fairly constant throughout the year usually ranging between 0 and 50  $\mu\text{g/l}$  (Fig. 4).

Nitrogen is a major nutrient for plants and becomes available to the form of nitrate. Figure 5 illustrated the values for the sum of nitrate for the study period. Since nitrate are usually fairly low the curve probably gives a fair representation of relative nitrate values. The range of total nitrate and nitrites was between 0.3 and 2.5. The lower values occurred in July through October and improved through the winter. A decline began in January and continued through March. Concentration began to increase gradually in the spring and by June the values were higher than those from the previous year. Nitrate concentrations may be inversely related to water level as similar but opposite trends are noted in Figure 2.

Figure 6 shows the season's variation in pH measured over the study period. Values did not vary much usually ranging between 7.0 and 7.7. A decrease was noted in late December and again in April and May. At these times the pH value became as low as 6.5. Maximum values occurred in November and January when they reached 7.8. Except for the spring data pH seems to parallel total alkalinity.

Biodegradation characteristics presented as degradation and effluents concentrations in total effluent and effluents from water samples taken from Lake Atsugi. The 11th experiment is called 11th exp. among [20].

Figure 5

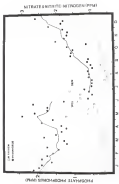


Figure 6: The relative loss of the hydrogen ion concentration (pH) at various sampling times from Lake Atica. The line is a 5-point moving average



Unfortunately orthophosphate-to-phosphorus was not determined in this study. Figure 5 represents the phosphate concentration present as total phosphorus. While this does not define orthophosphate availability it probably does give an index of it. Orthophosphate is the only form of phosphate derived from natural sources and is present in organic wastes and fertilizers (Verma 1981). Hence, it is probably the predominant form in Lake Allen. Phosphate-phosphorus concentrations were lowest in July and August 1984 (ca. 0.5 mg/l) and increased through December. Concentrations remained high into May and June 1985 and failed to return to the 1984 levels. This may have been an artifact of the lake level as it also failed to return to its previous July level. Also an increase in phosphate concentrations in April and May appear to correspond to a drop in the water level at the same time.

Phosphorus is a primary factor limiting production in aquatic ecosystems. Baller *et al.* (1980) found that P-concentrations below 0.1 µg/l were limiting to waterhyacinth growth. Above this concentration the plants absorbed P in luxury amounts. P-concentrations remained above this critical concentration throughout the year in Lake Allen. [ *excess*, therefore, that P does not become limiting to waterhyacinth at that site. The fact that phosphorus is lowest when plant density is highest probably reflects the increasing absorption of these luxury amounts by an increased plant standing crop. Wood (1975), however, found in a model simulation that phosphorus concentrations in Lake Allen appeared to be unaffected by waterhyacinth uptake or any other annual cycle. He further found that there was very little decrease in phosphorus in the direction of flow across the waterhyacinth mats, as hypothesized rather than diffusion may

be more limiting to plant species than phosphates since stronger winter peaks and summer minima were apparent in annual nitrogen cycles and nitrogen-fixing drops in the nitrate concentration occurred across the north. Gavigan et al. (1981) found that phosphate-phosphorus concentrations above 50 µg/l were not significantly affected by the growth of waterhyacinths but both nitrate-nitrogen and ammonia-nitrogen were. They further found that the N:P ratio of aquatic plants was 3-5:1.

Potassium concentrations (Fig. 7) remained fairly constant and did not show any strong seasonal variation. Values between June and December generally ranged between 2 and 4 mg/l. Concentrations increased somewhat from December through February and an almost decline occurred in March and April. By June potassium concentrations were about the same as they had been the previous year.

Sulfates (Fig. 7) were extremely variable but a bimodal tendency was observed. Concentrations appeared to be maximum in the fall and spring and minimum in the winter and summer. These plants take up relatively little sulfate compared to the most variable (Gutten 1972). This pattern is probably due to factors other than waterhyacinth growth.

#### Temperature and Solar Radiation

Figure 4 indicates the weekly maxima, minima, and mean air and water temperatures at Lake Alice during this study. Krilling et al. (1980) found that maximum growth of waterhyacinths was favored at water temperatures of 25-30°C. Water temperatures greater than 30°C were lethal and growth decreased linearly as temperatures were reduced to 15°C. In comparisons of plants exposed to 30°C days, 30°C nights with plants exposed to 30°C days, 10°C nights they found that the plants exposed to the lower nighttime



Figure 2: Polystyrene and styrene ligand concentrations of water samples taken from Lake Alice. The Y-axis represents ligand binding enthalpy.

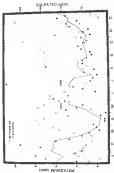
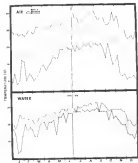


Figure 8. Maximum, minimum, and surface weekly air and water temperatures at Lake Okech from late June 1974 through June 1975. The winter air temperatures were consistently near during this study period.



air temperatures had photosynthetic rates 75-100% lower during the day. They also found that starch accumulation in the chloroplasts of 10°C plants was 2.6 times greater than the 30°C plants. They attributed this to the failure of the plant to translocate the previous day's starch accumulation from the chloroplasts...

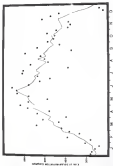
During the period of this study water temperature ranged between 10°C and 32°C except for two weeks in January when the weekly means were recorded as about 6°C. The median water temperature was never less than 10°C nor more than 31°C. The highest means occurred in late August and early September and the lowest means occurred in December and January. The optimum median temperatures (25-30°C as determined by Salpique et al.) occurred in June through October but median temperatures above 30°C occurred from mid-March through late November. It may be concluded that water temperatures were generally favorable for algaecyrtis growth most of the year although winter lows in December and January probably hindered growth. The lower limit (minimum) of 25-30°C was never approached so it is not reasonable to expect a summer decline resulting from high water temperatures.

Air temperatures ranged from a minimum of 55° in December and January to a maximum 41°C in August. The median weekly temperature was never less than 10°C nor greater than 30°C. Maximum temperatures, however, were consistently less than 30°C from early November to late April. Summer temperatures were relatively constant and averaged about 33°C. The winter was comparatively mild with only 3 days having minimum temperatures of 0°C or less. Six of these freezes occurred in December and 2 occurred in January. None were serious enough to severely damage the algaecyrtis beds. The only detectable effect noticed was a browning of the leaf tips on some of the larger plants.

Even though frost did not severely damage the plants in the winter the effect of the low temperatures may have been that of inhibiting translocation of starch as described previously. Winter daytime temperatures were generally quite warm but nighttime temperatures often fell to the 10°C range or below. If photosynthetic rates and carbohydrate translocation are reduced in this temperature regime a reduction in growth would be expected during this time. Beck (1981) found that plants grown at 4-4°C nights and 4-4°C days (16:8 L:8 photoperiod) grew very little (in 1982 during a 85 day test). Those grown at 26.7°C days and 4-4°C nights did only slightly better (ca. 25%) while those grown at 26.7°C days and nights increased the most (ca. 100%). Apparently minimum nighttime temperatures have a substantial effect on waterhyacinth growth and even though daytime temperatures may be warm growth may be suppressed. The inability of the plant to translocate starch in these low nighttime temperature conditions along with the subsequent reduction in photosynthetic efficiency seem to be the only explanation available for this phenomenon and is probably a result of an interaction between temperature effects and physiological mechanisms (Gardling et al. 1990).

Figure 5 illustrates the annual curve for solar radiation during the period of this study. The data is represented as daily averages for the period between sampling dates and is in terms of calories/cm<sup>2</sup>-(hourly) & a small increase in solar energy is indicated between the winter months and late spring and appears to be at a maximum in early June. This is followed by a gradual decline which continues throughout the remainder of the year and the minimum occurs at about the winter solstice. The summer maximum does not seem to occur at the summer solstice and measurements in late June, July, and August tend to be lower than would be expected based on day length

Figure 8-- Solar radiation data from the University of Florida space  
 from May 1981 through April 1983. Each point represents a  
 daily average reading. A one-day period solar radiation  
 begins to arrive before the summer solstice as a result of  
 atmospheric cloud cover associated with summer rain. The  
 shift of energy flux from atmospheric clouds are about  
 consistent on day (data from Dr. E. A. Farnett.)





clouds. This is probably the result of cloud cover associated with frequent afternoon thunderstorms common to this part of Florida during the summer (see rainfall in Figure 2).

### Microphytobenthic Productivity

Figures 18 and 19 (Tidegate journal) curves for the productivity of small and large waterhyacinths. Incident solar radiation and ambient temperature curves for the two days in which this study was done are also given. This data is the result of induced  $O_2$  gas analysis described in the methods section. This study was carried out cooperatively with Sandra Brown, Don Kopper, and DDT Wilson and it was agreed that each investigator would use the results freely in his research dictated. Even though this agreement was made I do wish to point out that this is not entirely my own material.

Gross primary production of the large plants (Fig. 18) was determined to be  $18.2 \text{ g C/m}^2/\text{day}$ . Respiration was estimated at  $11.2 \text{ g C/m}^2/\text{day}$  with the assumption that  $1 \text{ g C/m}^2 = 18 \text{ kcal}$  (these figures are transformed into  $192 \text{ kcal/m}^2/\text{day}$  and  $132 \text{ kcal/m}^2/\text{day}$ ). This indicates a value of  $60 \text{ kcal/m}^2/\text{day}$  for the net primary production. The ratio of this value and the incident solar energy indicates a net efficiency of 1.45. This translates into a net gain of  $43.65 \text{ gm organic matter}$  (assuming  $1 \text{ gm OM} = 4.5 \text{ kcal}$ ). Since the standing crop was  $2740 \text{ gm/m}^2$  is a net gain of  $8.62\%$  for the 24 hour period is estimated (9.82% standardizing to the  $4000 \text{ kcal solar radiation measurement of the small plants}$ ).

The gross primary production of the small plants (Fig. 19) was  $15.4 \text{ g C/m}^2/\text{day}$  ( $180 \text{ kcal/m}^2/\text{day}$ ). Respiration was estimated at  $7.8 \text{ gm C/m}^2/\text{day}$  ( $96 \text{ kcal/m}^2/\text{day}$ ) and net primary productivity at  $8.6 \text{ gm C/m}^2/\text{day}$  ( $100 \text{ kcal/m}^2/\text{day}$ ). The net efficiency for the small plants then is also 1.45. Since the standing crop is smaller this represents a relatively larger organic matter gain. The net productivity of  $86 \text{ gm C/m}^2$  equals an organic matter gain

Figure 18. Binned curve for large waterbody productivity determined from  $\text{CH}_4$  gas exchange measured in Lake Erie with an infrared  $\text{CH}_4$  gas analyzer. Respiration rates were determined from the average night-time values. Gross production is defined as the area under the curve above the respiration line. Net production is the area under the curve above the compensation point ( $0 \text{ g/lr/hr}$ ). The lower curves represent solar energy and temperature.

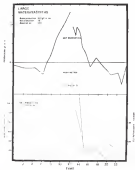
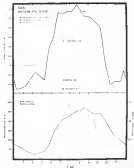


Figure 11: Stensal curve for small waterpocket productivity. See Figure 10 for explanation.



of 12-16 g/m<sup>2</sup> or an increase of approximately 2.0% (Bacon, 1966), one would expect the small plants to increase relatively more rapidly than the large plants.

The reasons for this difference are many. The increased metabolic load on the larger plants due to the larger standing crop results in a lower gross primary productivity/respiration ratio (1.46 vs. 2.04). This ratio at steady state is 1.00 which indicates that the larger plants are closer to steady state than the smaller ones. This refers that a greater portion of the gross production is spent in maintaining existing plant structure than in producing new material. This may be important in biological control considerations for a herbivore which merely removes leaf tissue without doing damage to the growing portion of the plant may tend to restrict ultimate growth.

Even though the total metabolic load was greater in the large plants the respiration per gram plant biomass was more than double in the smaller plants (see Table 5). This may be an indication of a more active metabolic rate associated with a faster growth rate.

Intraspecific competition for light may be another factor affecting the observed differences in growth rates. The leaf area index of the large plants was more than twice that of the small plants. The total amount of photosynthetic tissue was 2 times greater in the large plants and the leaf (petiole+stems) tissue was 5 times greater. In spite of these large differences net efficiencies were equal and gross efficiency was only 6% greater in the large plants. Hence, this greater amount of photosynthetic tissue is probably not as effective per unit as is the smaller amount of the small plants. In fact the gross productivity/gm

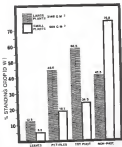




leaf tissue of the large plants is only 50% of that of the small plants even where differences in solar radiation are taken into account. The contribution of the photosynthetic layer to the petioles is not well understood but it is thought to be of minor importance in primary production (Salisbury *et al.* 1972). Further Salisbury *et al.* (1970) found that the light was rapidly extinguished beneath the upper canopy (ca. 70% at mid-height), hence the primary function of petioles is probably the supportive function of leaf display and the leaf tissue is probably photosynthetically more important than the total photosynthetic tissue. Table 5 lists the various metabolic comparisons standardized with regard to the leaf area index, photosynthetic tissue, leaf tissue, and standing crop. In all cases gross primary productivity is greater in the small plants than in the large ones even though the reverse is true strictly on a per unit area basis. The fact that the amount of leaf tissue present is 8 times greater in the large plants while the 60% leaf tissue is 40% less indicates that the increased leaf area interferes with light reception and probably results in a greater diversion from potential productivity.

The ratio of plant parts (Fig. 12) may be important in terms of supervised photosynthetic processes and may partly account for the difference in growth rates. As mentioned previously the petioles function in displaying the leaves but probably do not contribute greatly to photosynthesis. Hence, even though they are necessary, they represent a substantial metabolic cost to the plant. Petioles account for 40% of the weight of a large plant and only 16.7% of a small plant. A considerably greater portion of the small plant is non-photosynthetic in nature than

Figure 12 A comparison of the standing crop and proportions of the plant parts for the large and small *Artemisia* plants used in the productivity studies.



of the large plant (760 vs. 825). The ratio of non-photosynthetic to gross photosynthetic tissue (Table 5) is over 4 times greater in the small plants than that of the large plants. This non-photosynthetic tissue is primarily roots. Hence, the small plants are probably more efficient at absorbing nutrients to supply the photosynthetic and metabolic processes involved in growth and production. All of these factors are probably responsible for the faster growth rate of the small plants.

Because of the difficulty of measuring the data discussed here, replications were not possible at this time. As a result, statistical comparisons of the differences observed between the two types of plants could not be made. In spite of this, such direct methods of measuring productivity are far superior to traditionally used indirect measures such as the estimation of changes in standing crop by periodical harvesting. The latter method is often easily repeated and, as a result, may be statistically more appealing. The technique employed here, however, has the advantage of stoichiometric interpretation without the necessity of transferring the plants to an artificial laboratory situation as is usually required in metabolism studies.

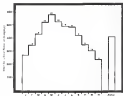
### Seasonal Variation in *Phytolacca* Tissues

Virtually all parameters associated with photosynthesis showed strong seasonal tendencies. Plant height, leaves per plant, leaves per unit area, area per leaf, leaf area index, area per petiole, petiole area index, and total leaf area index show seasonal seasonal ranges but these could vary in time depending upon the parameter measured.

Plant height (Fig. 14) seems to follow water potential curves but lags a month or two behind. Figure 15 shows average daily water potential for Lathropia on a monthly basis at 8 to 12 year averages. The data for the period of this study generally agrees with this (Figure 6). Maximum water potential occurs in late May or early June but maximum plant height (mean) is not achieved until late June and July. Minimum water potential occurs in December but plant height does not reach its lowest level until late January.

The number of leaves per plant (Fig. 16) appeared to be extremely variable. At the beginning of the study (May) the range was between 6 and 7 leaves per plant. The following May, however, it failed to return to this level (range 4-5). A decline was observed for this parameter throughout the summer followed by an increase in September. The gradual decline in the fall and winter seemed to parallel the decline in water potential but a sharp spring increase did not occur. This is explainable in terms of plant density and leaf density (Figs. 14 and 15). Even though the number of leaves per plant was low in the spring the number of leaves per square meter was at a maximum because plant density was high during this time. It may be concluded then that a plant has the greatest number of leaves in the summer when it is at its maximum height but the maximum

Figure 10 Average daily solar radiation values per month for Galveston, Texas- the figure above each bar represents the number of years the data are based upon. Adapted from the Climatic Atlas of the United States, U.S. Dept. of Commerce



## Figures 1a

Area's morphological change to the average height of the untransformed plants in the same size at each time. Area was assigned to the height of the largest leaf over the life of the plant relative to the size of the plant in its smallest to the present. The area is derived from all plants included in the first 8 200 of region. The dotted line represents the change in leaf area in untransformed vegetation (see Table 2)





Figure 15

Group's variability in the number of leaves per whole-plant plot, from the study area. The means are derived from weekly sampling and represent estimates from all plants contained in three 6 m<sup>2</sup> samples. Only leaves which had developed were counted. The dotted line represents predicted values based on multivariate regression equations (see Table 3).

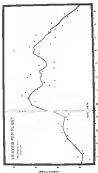
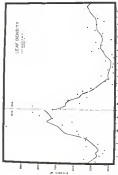


Figure 16

Actual change in half density as determined from each's sample, taken as the study area. Each point represents a new half on the basis of 'start' to end of days 8-111 in sample. The dotted line represents predicted values based on multivariate regression equations (see Table 1).



leaf density occurs in the spring when the plants are at their maximum density. Leaf density appeared to return very near the May 1988 level in May 1989.

Plant height, plant density, leaf density, and leaves per plant appear to be interrelated. It is confusing to consider any one of these as an indicator of photosynthetic production. A more valuable index is the leaf area index which takes into account the average area per leaf and the leaf density. Figure 17 represents the curve for the average area per leaf. This appears to be similar to the plant height curve but does not show the brief period of decline in the late summer. A single distinct peak occurs in July. The leaf area index is the product of the average area per leaf and the number of leaves per square meter and is represented in Figure 18. The leaf area index shows a strong increase in the spring actually beginning as early as February. A peak occurs in May as a result of both decreasing area per leaf and a high leaf density. A secondary peak occurs in July and seems to be due only to the increase in the area per leaf. A rapid decline occurs thereafter through early October. An increasing trend is observable in October but drops off very sharply within a two week period in November. The first cold weather (<4°C) occurred at this time and was apparently responsible for this. It is not really apparent what caused the short term rise in the leaf area index prior to this decline but a number of factors may be responsible. Leaf density was showing a steady increase while the area per leaf decreased slightly. Surface air temperatures appeared to increase somewhat at the time the net phosphate concentrations were increasing. The leaf area index reached its maximum in January following the last two frosts of the year (Dec 14 & 16) but this depression lasted only a few weeks and was

1

mentary and nonindigenous fish. In the  
one fish containing a parasite, the fish  
was identified as *Caprosoma* sp. (family  
Caprosomidae). It is noted that 11% of specimens were  
parasitized with only one fish harboring a large, very young  
*Caprosoma*. It is important to note that none of the collected fish

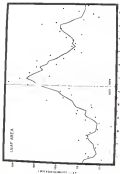
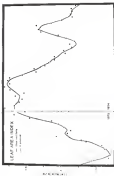




Figure 10. Leaf area index of the winterwheat production in Iowa. After each year, represents the product of the leaf density and average height and the average area the leaf is absorbed from the limited carbon (Figure 14 and 15). The dashed line represents predicted plant based on self-correlation regression statistics. (See Table 7)



followed by a sharp increase. On the whole the leaf area index seems to follow solar radiation cycles. Cold weather causes a depression in the leaf area index but the effect was short due to the relatively mild winter. The strategy of the plant seems to be to maximize photosynthetic capacity. This is done first in the spring by increasing leaf density and effort production followed by an increase in leaves per plant and leaf size in the summer as intraspecific competition becomes more intense.

As was discussed previously, the importance of the petiole to photosynthesis is not known. It is assumed, however, to contribute little. For this reason the petiole area index has not been graphed. The area per petiole is usually very close to the area per leaf. Hence, the total leaf area (pseudostem and petiole) is approximately twice the leaf area and the total leaf area index is approximately twice the leaf area index. All three (leaf area, petiole area, and total leaf area) strongly parallel the curve for mean maximum height (Fig. 14).

### Seasonal Variation in Plant Density

Plant density (Fig 18) did not seem to follow the same trends as the various attributes of photosynthetic tissue. A major peak occurred in late April when the density reached 108 plants per square meter. This was followed by an equally abrupt decline in May. By June the density was between 20 and 50 plants per square meter and it remained in this range until September. At this time the density began to increase and a secondary peak of 100 to 140 plants per square meter was achieved in early January. This level dropped slightly in February but the spring increase began in early March.

Figure 10

Actual change in plant density is determined from weekly census means. In the study area, each point represents a 1-acre divided into 1000 sub-plots. The first three 1/1000 a sample, only attacks with some root development were marked as distinct plants. The dotted line represents predicted values based on nonlinear-like regression equation. (see Table 1)

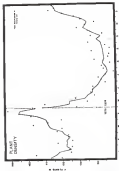


Fig. 1. Relationship between seed density and number of seeds. The plot shows the distribution of seed density (x-axis) and number of seeds (y-axis) for the 1000 simulated populations. The legend indicates the seed density scale.

These observations were somewhat surprising as a decrease in density was expected as solar radiation levels fell and temperatures became colder. Plant density was definitely higher in the winter, however, than in the summer. This appears to be related to the leaf area index and plant height. The average weekly frequency distribution for the various plant height classes for each month is shown in Figure 26. In January the distribution was narrow (range 50 cm) and skewed towards the smaller plants. The dominant size class was 21-30 cm which contained approximately 32 plants (44%). Taken together with the two smaller size classes, 80% of the plants were found to be less than 40 cm during this month.

In February the distribution was narrower yet (range 50 cm) but the predominant size class was larger (31-40 cm) and contained 31% of the plants. Still the greater proportion of the plants were smaller than the predominant class (44%) and taken together with the predominant class represented 75% of the population.

In March the range of plant height increased (80 cm) and there was a lack of a single predominant size class. Four size classes (21-30, 31-40, 41-50, 51-60) accounted for 22%, 34%, 25%, and 19% of the population respectively or 80% of the population collectively. By April when the greatest increase in density occurred the size classes appeared to be nearly evenly distributed. The predominant class was 31-40 cm in height and contained 26 plants (34%) and together with the 41-50 cm class accounted for 42% of the population. Smaller size classes contained 25% of the population and larger plants accounted for 33%.

In May the distribution seemed to differentiate. Two modes were apparent, the first in the 41-50 range and the second in the 71-80 and 81-90 ranges.

Figure 26 Average monthly counts of the number of plants included in each plant height class per square meter. The monthly values were derived from the averages of all the weekly samples taken during a given month. The dark vertical bars represent the frequency of damage to the different height classes.



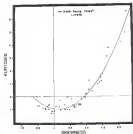


The latter two classes comprised 65% of the population and 40% were smaller. Approximately 50% of the population was larger which was similar to the previous month. By June this subpopulation of small plants began to disappear and the distribution was skewed strongly towards the larger size classes. The 80-100 and 100-110 cm classes were co-dominant with 60% of the population, the smaller classes comprised 34% of the total and the larger only 6%. This continued in July and the same two size classes represented 65% of the population. The contribution of the small plants was minor with only a 10% representation. The predominant size class was 100-110 cm in July and was the maximum height achieved by a dominant class. The distribution was similar in August and September but the predominant class was 80-100 cm in both months.

In October the predominance of the larger size classes was beginning to decrease and the smaller plants were becoming more important. A net increase in density occurred which was apparently responsible for the increase in the smaller size classes. The two predominant classes (90-100, 100-110) comprised only 35% of the population. This trend continued in November but the two predominant classes were smaller (70-80, 80-90) and 40% of the plants were smaller, by December the predominant class was 70-80 cm and the frequency distribution was broad. Six classes (20-80 cm) were co-dominant.

Statistics for skewness (asymmetry) and kurtosis (peakedness) were determined for each weekly frequency distribution according to the methods described by Sokal and Rohlf (1969). Kurtosis was plotted as a dependent function of skewness and a hyperbolic regression fitted to the data (Fig. 2). Positive values for skewness indicate that the distribution is skewed towards the - end (high values in the distribution). Negative

**Figure 11** Statistics of skewness and kurtosis [peaking] derived from each weekly frequency distribution of plant density by height classes. This figure indicates that as the frequency of plants becomes skewed towards the larger height classes the degree of peaking in the distribution increases sharply (i.e., the diversity of height classes represented decreases).



values indicate that the distribution is skewed left (towards low values). Positive values for kurtosis indicate a high degree of peaking where a few classes contain most of the individuals in the distribution, negative values indicate a broad distribution with less distinct peaks. Both skewness and kurtosis are approximately 0 in a normal distribution. The regression indicates that when the population is not strongly skewed towards the larger size classes the distribution tends to be equal or depressed with several classes well represented. As the degree of skewness towards the large size classes increases, however, the population shows much stronger peaks indicating the increased predominance of a few size classes. This supports the contention that the increased dominance by the large plants results in a loss of the smaller size classes and a decrease in density.

In general, then, as the predominant size class becomes larger there appears to be a loss of plants in the smaller size classes and plant density decreases. This is further illustrated in Figure 22 where each weekly frequency distribution is plotted from January through December in a three dimensional manner. This is particularly true in the summer when the largest plants are also the predominant class. As the leaves from the larger plants die the small plants become better represented and the density increases. Density, then, appears to be auto-regulatory and responds to the changes in the canopy. Even though the photosphere is decreasing the amount of light may increase in the lower canopy as the leaves of the larger plants die off. This may stimulate offset production as is evidenced by the close inverse association between plant height and plant density. There appears to be an optimum, however, and this may have occurred in April. At this time the degree of intraspecific

Figure 21

The empty rectangular light class frequency distribution plotted along diagonally on a log scale. The horizontal axis represents the classes increasing from left to right. The vertical axis represents density. The number of plots in each light class are square meter. The label axis, perpendicular to the plane of the paper, represents the density.

18	2	4	7	9	10
15	1	3	5	6	8



FIGURE 1. A large tree trunk with thick, deeply furrowed bark, showing the characteristic texture of the wood. The illustration is a detailed black and white drawing, likely a woodcut or engraving, showing the intricate patterns of the bark and the solid, textured interior of the trunk.

shading was not as intense as to select for only the larger height classes. Taller radiation was weaker and a dramatic increase in density resulted. Following this, as the plants became taller and the average area per leaf decreased, intraspecific competition substantially selected for the plants which could maximize their energy budgets, namely the larger height classes. As these large plants became larger the light available to the smaller plants became less. This resulted in the loss of the smaller size classes and the skewed distributions observed in the summer. As a result of constant time, a decrease in density does not necessarily indicate a reduction in the operation of a r-strategyistic plant. This could easily be demonstrated by persons evaluating the effect of insects on waterhyacinths.

#### Seasonal Variation in the Standing Crop

Standing crop was not measured directly on a weekly basis. However, biomass samples were taken in December 1979 during the period of this study and in April, May, June, July and August 1979 after weekly data collection were terminated. From these biomass samples the average weight per plant was estimated and is plotted against the average height (measured at the same time) in Figure 23. An exponential regression was fitted to this data and the regression formula derived. The correlation coefficient for this regression was 0.92 with 10 degrees of freedom and is highly significant ( $<0.01$ ). The estimates for average height from the original weekly samples were entered into this regression equation to determine the estimated average weight per plant. This value was multiplied by the plant density for the same sampling period to obtain an estimate of the standing crop per square meter in terms of gross dry weight. These

Figure 12 Average weight per plant as a log function of the average plant height. Data from biomass samples taken from Lake Kizir.



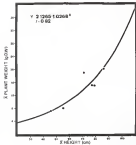
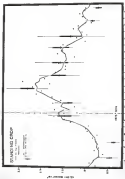


Figure 28:

Simulated crop values, both anticipated and real, from late June through the initial September estimates derived from the current values for rainfall, from day 124 through April 1975 using the equation in Figure 3) to determine an estimated plant weight. These values multiplied by plant density to obtain an estimate for standing crop. The vertical bars represent actual measurements from day 0.25 of anthesis (late mid-June) from April 1975 through February 1976. The dotted line represents predicted values from multivariate regression analysis (see Table 1).



estimates are plotted in Figure 24. Subsequent actual measurements taken from April 1975 - February 1976 are also plotted (vertical bars) and conforms very well with the estimated curve. As a result I feel that the estimated curve is a fairly realistic representation of actual conditions.

Standing crop was lowest in January and February when it ranged between 400 and 1000 gm DW/m<sup>2</sup>. A period of exponential growth began in March and continued through April; the discontinuity of the curve at the end of April is due to differences between the initial measurements in May 1974 and the final measurements in 1975. It is therefore not apparent whether this exponential trend continued; it may not seem so, however, because there was a drop in biomass between April and May of 1975 in the actual biomass samples. Following this decline a nearly linear rise occurred through late June. During this period of active growth the growth rate was highest in March and April. The daily increment factor (see back title) for this period (5 March - 23 April) is estimated at 1.25-4) 25 per day). The same value for the period between 1 May and 18 July is 1.813 (3.45 per day). The average monthly values for daily increments are listed in Table 6.

Following the peak in July a rapid decline occurred. This was followed by a stable period in mid-September. A gradual decline began the first part of October and continued through January. Biomass remained stable in February before beginning a spring resurgence.

Survivability, the greatest monthly declines did not occur during the entire season but rather in October and November. This may have been due to heavy damage by *Artemia* larvae which occurred at that time. The period of maximum growth (April) corresponds to the greatest monthly

Table 6. Average daily rates of change in biomass from initial and final monthly values.

Month	Standing Crop		Interval (Days)	Daily Increment <sup>a</sup>
	Est. Estimate	Less Estimate		
Jan	162	100	21	0.003
Feb	190	157	20	0.003
Mar	225	200	23	0.001
Apr	249	193	26	0.002
May	279	204	26	0.003
Jun	292	210	22	0.003
Jul	290	202	26	-0.003
Aug	283	192	22	-0.004
Sep	270	180	21	0.004
Oct	260	163	26	-0.002
Nov	250	161	21	-0.002
Dec	247	159	20	-0.002

<sup>a</sup>Equals  $\frac{I - F}{T}$  where  $I$  = Initial,  $F$  = Final estimate,  $T$  = Interval estimate

response to water reduction (see Fig. 1), the drop in May was probably due to the loss of small plants as a result of increased intraspecific competition. There appears to be two growth phases, the early spring phase due to both increasing plant density and individual plant growth and the early summer phase due to individual plant growth only. This seems to parallel the theory of cyclic  $r$  and  $K$ -selection and will be discussed later in this section.

#### Damage by *Armsia arvensis*

Lawns of *Armsia arvensis* cause considerable damage to the subnivean plants by boring into the leaves and rhizomes. Eggs are laid in masses usually on the pseudostolons and upon emergence the maggots enter the leaves or move to the base of the plant and feed on the tender wrapper leaves. As they become larger (ca. 4th instar) they bore into the petioles. Prior to this time they primarily feed externally on the photosynthetic tissue. By the 5th instar they are capable of killing the leaves and may bore into the rhizomes. At first, damage to the rhizomes occurs at the apical tip but later the 5th and 7th instars tunnel into it creating large tunnels and possibly fragmenting the plant. Damage by the larger larvae often results in the death of the plant.

Figure 25 illustrates the leaves damaged by *A. arvensis* as a percentage of the total leaf density. This figure represents total leaf damage and does not distinguish between external feeding and petiole boring. Figure 26 also illustrates the percentage of the plants with rhizome damage. Again, the degrees of damage are not distinguished. Figure 28 illustrates monthly averages for rhizome damage by plant size classes.

Leaf damage (Fig. 25) was very low in the summer as was the larval

Figure 25

Percentage of the forest and rhyzomes of the subterranean bats  
found in an damaged through feeding activity of *Arctura domus*  
in Lake Africa





populations. An increase in damage was apparent beginning in July and continuing through November when a peak of approximately 25% occurred. A decline followed through December until late January when the damage ranged between 5 and 10%. It remained at this level through February and March with a brief increase in April. By mid-May the level of damage was somewhat greater than the previous year.

Wilcox damage closely paralleled leaf damage but was generally lighter, peaking in November when 45% of the plants had wilcox damage (Fig. 26). Wilcox damage was very low from May through September (Figure 26). An increase was apparent in October but most of the damage was minor. Most of the severe damage occurred in November, December, and January. By spring the relatively low larval population coupled with the high plant density resulted in relatively low levels of damage. The increase noted in April was primarily minor damage.

The frequency of attack of a given plant size class roughly corresponds to the frequency of that size class (Figure 25). This is generally true throughout the year except in December and January when the smaller plants are more abundant but most of the damage occurs in the larger plants. This may be partly responsible for the loss of plants in the larger classes apparent between December and January. Otherwise it appears that there is no selection by the insect for the size of plant attacked. Larger plants may be attacked more frequently at certain times but this is probably due to the fact that they are older and have been exposed to attack for a longer period of time. If the selection of a plant in a given size class by a larva is a random process then the frequency of attack within that class should correspond to the relative abundance of that class within the frequency distribution. Without further analyses this appears to be the case.

### Results of the Multivariate Analysis

The results of the multivariate regression analysis are summarized in Table 2. The equations for each dependent variable may be derived from this table by reading across the row according to the form of the general model. All regressions were highly significant with a probability of a greater  $F$  occurring by chance of  $< 0.001$ . Some of the regression coefficients were not significant at the 0.05 level but were included if the probability for the null hypothesis (see 4-6) was less than 0.10.

Water potential and minimum air temperature were the most important variables in the models for standing crop, plant height, leaf area index, and leaves per plant. Since all of the climatological variables were highly correlated (see Table 1) the inclusion of these two reflects the importance of climate to the maintenance of the waterpotential stand.

Nitrogen effects were variable depending upon the model. Nitrogen was important only in the equations for standing crop but the coefficient was negatively significant at the 0.05 level. This infers that high levels of nitrogen were associated with lower standing crop values and vice-versa. This previous relationship was somewhat unexpected since the nitrogen concentrations should drop as biomass increased and greater quantities of nitrogen are absorbed. Phosphate-phosphorus was included in the models for plant height, leaf density, and plant density. The coefficient for plant height was negative and properly reflects the uptake of phosphorus as height increases. The positive coefficients for leaf density and plant density indicate that these values were high at the time that phosphorus concentrations were high. Potassium was a significant factor in the same three models but the relationship was reversed. High potassium concentrations corresponded to low leaf and plant density values and to high values for plant height.

Table 1. Summary of data

Table 1. Summary of data. The table shows the results of the analysis of variance for the different factors. The first column shows the factor, the second column shows the number of levels, the third column shows the number of observations, and the fourth column shows the degrees of freedom. The fifth column shows the F-value, and the sixth column shows the p-value. The seventh column shows the adjusted R-squared value, and the eighth column shows the adjusted F-value.

Factor	Number of levels	Number of observations	Degrees of freedom	F-value	p-value	Adjusted R-squared	Adjusted F-value
Factor 1	2	10	1	10.0	0.01	0.10	10.0
Factor 2	3	15	2	5.0	0.05	0.05	5.0
Factor 3	4	20	3	3.3	0.10	0.02	3.3
Factor 4	5	25	4	2.5	0.15	0.01	2.5
Factor 5	6	30	5	2.0	0.20	0.00	2.0
Factor 6	7	35	6	1.7	0.25	0.00	1.7
Factor 7	8	40	7	1.5	0.30	0.00	1.5
Factor 8	9	45	8	1.3	0.35	0.00	1.3
Factor 9	10	50	9	1.1	0.40	0.00	1.1
Factor 10	11	55	10	1.0	0.45	0.00	1.0
Factor 11	12	60	11	0.9	0.50	0.00	0.9
Factor 12	13	65	12	0.8	0.55	0.00	0.8
Factor 13	14	70	13	0.7	0.60	0.00	0.7
Factor 14	15	75	14	0.6	0.65	0.00	0.6
Factor 15	16	80	15	0.5	0.70	0.00	0.5
Factor 16	17	85	16	0.4	0.75	0.00	0.4
Factor 17	18	90	17	0.3	0.80	0.00	0.3
Factor 18	19	95	18	0.2	0.85	0.00	0.2
Factor 19	20	100	19	0.1	0.90	0.00	0.1
Factor 20	21	105	20	0.0	0.95	0.00	0.0
Factor 21	22	110	21	0.0	1.00	0.00	0.0
Factor 22	23	115	22	0.0	1.00	0.00	0.0
Factor 23	24	120	23	0.0	1.00	0.00	0.0
Factor 24	25	125	24	0.0	1.00	0.00	0.0
Factor 25	26	130	25	0.0	1.00	0.00	0.0
Factor 26	27	135	26	0.0	1.00	0.00	0.0
Factor 27	28	140	27	0.0	1.00	0.00	0.0
Factor 28	29	145	28	0.0	1.00	0.00	0.0
Factor 29	30	150	29	0.0	1.00	0.00	0.0
Factor 30	31	155	30	0.0	1.00	0.00	0.0
Factor 31	32	160	31	0.0	1.00	0.00	0.0
Factor 32	33	165	32	0.0	1.00	0.00	0.0
Factor 33	34	170	33	0.0	1.00	0.00	0.0
Factor 34	35	175	34	0.0	1.00	0.00	0.0
Factor 35	36	180	35	0.0	1.00	0.00	0.0
Factor 36	37	185	36	0.0	1.00	0.00	0.0
Factor 37	38	190	37	0.0	1.00	0.00	0.0
Factor 38	39	195	38	0.0	1.00	0.00	0.0
Factor 39	40	200	39	0.0	1.00	0.00	0.0
Factor 40	41	205	40	0.0	1.00	0.00	0.0
Factor 41	42	210	41	0.0	1.00	0.00	0.0
Factor 42	43	215	42	0.0	1.00	0.00	0.0
Factor 43	44	220	43	0.0	1.00	0.00	0.0
Factor 44	45	225	44	0.0	1.00	0.00	0.0
Factor 45	46	230	45	0.0	1.00	0.00	0.0
Factor 46	47	235	46	0.0	1.00	0.00	0.0
Factor 47	48	240	47	0.0	1.00	0.00	0.0
Factor 48	49	245	48	0.0	1.00	0.00	0.0
Factor 49	50	250	49	0.0	1.00	0.00	0.0
Factor 50	51	255	50	0.0	1.00	0.00	0.0
Factor 51	52	260	51	0.0	1.00	0.00	0.0
Factor 52	53	265	52	0.0	1.00	0.00	0.0
Factor 53	54	270	53	0.0	1.00	0.00	0.0
Factor 54	55	275	54	0.0	1.00	0.00	0.0
Factor 55	56	280	55	0.0	1.00	0.00	0.0
Factor 56	57	285	56	0.0	1.00	0.00	0.0
Factor 57	58	290	57	0.0	1.00	0.00	0.0
Factor 58	59	295	58	0.0	1.00	0.00	0.0
Factor 59	60	300	59	0.0	1.00	0.00	0.0
Factor 60	61	305	60	0.0	1.00	0.00	0.0
Factor 61	62	310	61	0.0	1.00	0.00	0.0
Factor 62	63	315	62	0.0	1.00	0.00	0.0
Factor 63	64	320	63	0.0	1.00	0.00	0.0
Factor 64	65	325	64	0.0	1.00	0.00	0.0
Factor 65	66	330	65	0.0	1.00	0.00	0.0
Factor 66	67	335	66	0.0	1.00	0.00	0.0
Factor 67	68	340	67	0.0	1.00	0.00	0.0
Factor 68	69	345	68	0.0	1.00	0.00	0.0
Factor 69	70	350	69	0.0	1.00	0.00	0.0
Factor 70	71	355	70	0.0	1.00	0.00	0.0
Factor 71	72	360	71	0.0	1.00	0.00	0.0
Factor 72	73	365	72	0.0	1.00	0.00	0.0
Factor 73	74	370	73	0.0	1.00	0.00	0.0
Factor 74	75	375	74	0.0	1.00	0.00	0.0
Factor 75	76	380	75	0.0	1.00	0.00	0.0
Factor 76	77	385	76	0.0	1.00	0.00	0.0
Factor 77	78	390	77	0.0	1.00	0.00	0.0
Factor 78	79	395	78	0.0	1.00	0.00	0.0
Factor 79	80	400	79	0.0	1.00	0.00	0.0
Factor 80	81	405	80	0.0	1.00	0.00	0.0
Factor 81	82	410	81	0.0	1.00	0.00	0.0
Factor 82	83	415	82	0.0	1.00	0.00	0.0
Factor 83	84	420	83	0.0	1.00	0.00	0.0
Factor 84	85	425	84	0.0	1.00	0.00	0.0
Factor 85	86	430	85	0.0	1.00	0.00	0.0
Factor 86	87	435	86	0.0	1.00	0.00	0.0
Factor 87	88	440	87	0.0	1.00	0.00	0.0
Factor 88	89	445	88	0.0	1.00	0.00	0.0
Factor 89	90	450	89	0.0	1.00	0.00	0.0
Factor 90	91	455	90	0.0	1.00	0.00	0.0
Factor 91	92	460	91	0.0	1.00	0.00	0.0
Factor 92	93	465	92	0.0	1.00	0.00	0.0
Factor 93	94	470	93	0.0	1.00	0.00	0.0
Factor 94	95	475	94	0.0	1.00	0.00	0.0
Factor 95	96	480	95	0.0	1.00	0.00	0.0
Factor 96	97	485	96	0.0	1.00	0.00	0.0
Factor 97	98	490	97	0.0	1.00	0.00	0.0
Factor 98	99	495	98	0.0	1.00	0.00	0.0
Factor 99	100	500	99	0.0	1.00	0.00	0.0
Factor 100	101	505	100	0.0	1.00	0.00	0.0
Factor 101	102	510	101	0.0	1.00	0.00	0.0
Factor 102	103	515	102	0.0	1.00	0.00	0.0
Factor 103	104	520	103	0.0	1.00	0.00	0.0
Factor 104	105	525	104	0.0	1.00	0.00	0.0
Factor 105	106	530	105	0.0	1.00	0.00	0.0
Factor 106	107	535	106	0.0	1.00	0.00	0.0
Factor 107	108	540	107	0.0	1.00	0.00	0.0
Factor 108	109	545	108	0.0	1.00	0.00	0.0
Factor 109	110	550	109	0.0	1.00	0.00	0.0
Factor 110	111	555	110	0.0	1.00	0.00	0.0
Factor 111	112	560	111	0.0	1.00	0.00	0.0
Factor 112	113	565	112	0.0	1.00	0.00	0.0
Factor 113	114	570	113	0.0	1.00	0.00	0.0
Factor 114	115	575	114	0.0	1.00	0.00	0.0
Factor 115	116	580	115	0.0	1.00	0.00	0.0
Factor 116	117	585	116	0.0	1.00	0.00	0.0
Factor 117	118	590	117	0.0	1.00	0.00	0.0
Factor 118	119	595	118	0.0	1.00	0.00	0.0
Factor 119	120	600	119	0.0	1.00	0.00	0.0
Factor 120	121	605	120	0.0	1.00	0.00	0.0
Factor 121	122	610	121	0.0	1.00	0.00	0.0
Factor 122	123	615	122	0.0	1.00	0.00	0.0
Factor 123	124	620	123	0.0	1.00	0.00	0.0
Factor 124	125	625	124	0.0	1.00	0.00	0.0
Factor 125	126	630	125	0.0	1.00	0.00	0.0
Factor 126	127	635	126	0.0	1.00	0.00	0.0
Factor 127	128	640	127	0.0	1.00	0.00	0.0
Factor 128	129	645	128	0.0	1.00	0.00	0.0
Factor 129	130	650	129	0.0	1.00	0.00	0.0
Factor 130	131	655	130	0.0	1.00	0.00	0.0
Factor 131	132	660	131	0.0	1.00	0.00	0.0
Factor 132	133	665	132	0.0	1.00	0.00	0.0
Factor 133	134	670	133	0.0	1.00	0.00	0.0
Factor 134	135	675	134	0.0	1.00	0.00	0.0
Factor 135	136	680	135	0.0	1.00	0.00	0.0
Factor 136	137	685	136	0.0	1.00	0.00	0.0
Factor 137	138	690	137	0.0	1.00	0.00	0.0
Factor 138	139	695	138	0.0	1.00	0.00	0.0
Factor 139	140	700	139	0.0	1.00	0.00	0.0
Factor 140	141	705	140	0.0	1.00	0.00	0.0
Factor 141	142	710	141	0.0	1.00	0.00	0.0
Factor 142	143	715	142	0.0	1.00	0.00	0.0
Factor 143	144	720	143	0.0	1.00	0.00	0.0
Factor 144	145	725	144	0.0	1.00	0.00	0.0
Factor 145	146	730	145	0.0	1.00	0.00	0.0
Factor 146	147	735	146	0.0	1.00	0.00	0.0
Factor 147	148	740	147	0.0	1.00	0.00	0.0
Factor 148	149	745	148	0.0	1.00	0.00	0.0
Factor 149	150	750	149	0.0	1.00	0.00	0.0
Factor 150	151	755	150	0.0	1.00	0.00	0.0
Factor 151	152	760	151	0.0	1.00	0.00	0.0
Factor 152	153	765	152	0.0	1.00	0.00	0.0
Factor 153	154	770	153	0.0	1.00	0.00	0.0
Factor 154	155	775	154	0.0	1.00	0.00	0.0
Factor 155	156	780	155	0.0	1.00	0.00	0.0
Factor 156	157	785	156	0.0	1.00	0.00	0.0
Factor 157	158	790	157	0.0	1.00	0.00	0.0
Factor 158	159	795	158	0.0	1.00	0.00	0.0
Factor 159	160	800	159	0.0	1.00	0.00	0.0
Factor 160	161	805	160	0.0	1.00	0.00	0.0
Factor 161	162	810	161	0.0	1.00	0.00	0.0
Factor 162	163	815	162	0.0	1.00	0.00	0.0
Factor 163	164	820	163	0.0	1.00	0.00	0.0
Factor 164	165	825	164	0.0	1.00	0.00	0.0
Factor 165	166	830	165	0.0	1.00	0.00	0.0
Factor 166	167	835	166	0.0	1.00	0.00	0.0
Factor 167	168	840	167	0.0	1.00	0.00	0.0
Factor 168	169	845	168	0.0	1.00	0.00	0.0
Factor 169	170	850	169	0.0	1.00	0.00	0.0
Factor 170	171	855	170	0.0	1.00	0.00	0.0
Factor 171	172	860	171	0.0	1.00	0.00	0.0
Factor 172	173	865	172	0.0	1.00	0.00	0.0
Factor 173	174	870	173	0.0			

Iron appears to be an important nutrient in at least three models. The coefficient for iron was negative in the equation for leaves per plant. The number of leaves per plant is correlated with standing crop (see Table 5), hence, the negative coefficient for iron can be taken to indicate uptake of iron as the plant biomass increases. The positive coefficients in the models for leaf and plant density indicate that iron concentrations are high when these two variables are high. High maximum plant and leaf densities occur early in the growing season (iron levels may be high because the plants have not yet affected it). The peak for plant density occurs immediately after the peak for iron concentration (see Figs. 4 and 16). This indicates that a causal relationship may exist between the two.

Potassium was included in the equation for plant height, leaf density, and plant density. A decrease in the potassium concentration between late February and late April (Fig. 3) corresponds to the peak for leaf and plant density and accounts for the negative potassium coefficient for these two variables. The positive relationship between potassium and plant height (Fig. 14) is not obvious by mere inspection of the data. The indication is that as potassium concentrations increase, plant height also increases. The effects of other important variables probably obscure this relationship between potassium and plant height.

Reproduction was significant in the model for leaf density. This was somewhat surprising since reproduction concentrations were relatively constant through the year (see Fig. 4). The coefficient for leaf density was negative but this inverse association is not obvious.

Sulfuric acid concentration ( $\mu\text{M}$ ) was included in the model for leaf area index with a negative coefficient. Values of  $\mu\text{M}$  had a narrow range





Table 9: Counterfactuals

	Reduction	Regulation	Abroad/In	IT	Industria	Land
Output per worker	-0.249 (0.0001)	-0.175 (0.0000)	-0.061 (0.0000)	-0.209 (0.0000)	-0.280 (0.0000)	-0.247 (0.0000)
Human capital	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)
Acc. Acc.	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)
Acc. H/L	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)
Acc. H/H	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)
Relative Savings	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)
Land savings	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)
Population	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)
Migration	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)
Trade	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)
Government	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)
Government	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)
Regulation	-	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)
Abroad/In	-	-	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)
IT	-	-	-	-0.000 (0.0000)	-0.000 (0.0000)	-0.000 (0.0000)
Land savings	-	-	-	-	-0.000 (0.0000)	-0.000 (0.0000)
Land savings	-	-	-	-	-	-0.000 (0.0000)

Table 3. Correlation coefficients ( $r$ ) between dependent variables. Values in parentheses represent the probability of a greater  $|r|$  under the null hypothesis.

	Standing crop	Plant height	Leaf area index	Leaves per plant	Leaf density	Plant biomass
Standing crop	1.000 (0.0000)	..	...	..	...	...
Plant height	0.186 (0.0001)	1.000 (0.0000)	...	..	..	..
Leaf area index	0.150 (0.0001)	-0.088 (0.0001)	1.000 (0.0000)	...	..	..
Leaves per plant	0.077 (0.0001)	0.198 (0.0001)	0.010 (0.0001)	1.000 (0.0000)	..	..
Leaf density	0.187 (0.0001)	0.076 (0.0001)	-0.195 (0.0001)	0.140 (0.0001)	1.000 (0.0000)	..
Plant biomass	0.191 (0.0001)	-0.168 (0.0001)	-0.187 (0.0001)	-0.168 (0.0001)	0.076 (0.0001)	1.000 (0.0000)



over the year but were generally lower in April and May (see Fig. 8). This may be the result of increased plant respiration during this phase of active growth. Respiration increases the  $\text{CO}_2$  concentration which reacts with water to form carbonic acid. Carbonic acid dissociates and increases the hydrogen ion concentration thus lowering pH. These changes are usually buffered by reacting with limestone to form carbonates and bicarbonates. This accounts for the correlation between pH and alkalinity [total carbonates and bicarbonates] in Table 5. The drop in pH, then, is probably a result of plant growth and not a cause of it.

Alkalinity was included in the plant height model but the coefficient was not significant. Sulfates were significant in the model for leaves per plant and had a positive coefficient. Significant correlations with sulfates include conductivity, magnesium, potassium and alkalinity. Overall, then, sulfates are probably an index of sulfate salts.

Water level was included in the plant height model with a negative coefficient and in the plant density model with a positive coefficient. Considering the water sources for Lake Alice low water levels probably result in a concentration of nutrients and high levels in a dilution. The negative coefficient for plant height indicates, then, that the effects are better when nutrients are low. Conversely the plants are most dense when nutrients are high. Significant negative correlations exist between water level and nitrogen and phosphorus.

Maximum water temperature was the most important variable in the plant density model and was negatively related to it. Hence, low maximum water temperatures indicate high densities.

In general, the models seem to indicate that the variables that

some as indices of biomass (see Table II) are regulated by climate as solar radiation and air temperature are most important. Leaf density and plant density appear to be regulated more by hydrologic conditions as various water quality parameters are implicated.

Predicted values were generated for each dependent variable based on the known independent variable values. Each has been plotted as an annual curve with the actual observed curve (see Figs. 14, 15, 16, 17, 18, and 19). Biomass estimates (Fig. 16) seemed to fit well in the winter, spring and fall but values were underestimated in the summer. This is probably because of the assumption of linear effects inherent in the model. As mentioned previously this assumption is probably not justified. Plant height (Fig. 14) was approximated fairly accurately. The observed drop in late August was not approximated, however, and an increase in late January was predicted which did not occur. This is apparently the result of a brief period of warm weather which, according to the model, should have resulted in a brief increase in height. Otherwise the included variables satisfactorily account for variations in height.

Leaves predicted for leaf area index produce a curve of approximately the same shape as the observed data (Fig. 18). The peak was not predicted until early June, however, where it actually occurred in mid-May. The predicted peak corresponds to the peak in solar radiation.

The predicted curves for leaves per plant (Fig. 19) and leaf density (Fig. 18) conform extremely well to the actual data. Plant density (Fig. 19) is also well represented but the spring peak is not as dramatic as was observed. This is probably because the change at this time was exponential and the model treats it as a linear function.

Overall, with the exception of standing crop and possibly leaf area index, the models produced reflect observed trends in the plant characteristics fairly accurately. More sophisticated modeling techniques could probably improve these fits if non-linear responses could be considered.

### Discussion

The object of this study was to determine the degree of effect of damage by downy down on various characteristics of the subterranean population. Neither leaf damage nor rhizome damage proved to be a significant factor in any of the models derived from the multivariate regression analyses (Table 7). The obvious conclusion based only on these analyses is that  $\lambda$ , downy down, did not effect the plants or, more precisely, did not account for a significant amount of the variation observed in the plant characteristics measured. Upon examination of the correlation matrix for the independent variables (Table 8), however, it is found that both leaf and rhizome damage are highly correlated with the climatological variables and with water level. Further, these correlation coefficients are all positive indicating that insect damage is high when sunlight, temperature, and water level are low. Because of these relationships it is not reasonable to exclude insect damage as an important factor since the correlated variables are important. If all of the variables were independent a term for insect damage may have been included in the models. In lieu of this independence the stepwise analysis first selects the parameter which best reduces the variability. Further parameters are used to account for the variability remaining after variability due to the first parameter is removed. When the first and second parameters are highly correlated the reduction of variability due to the first may also

removes the effects of the variable. In this case the variable variable is considered as not important and is excluded from the model. This may very well have been the case with insect damage. The effects of insect damage may have been obscured in this manner by the greater effects of sunlight, temperature, and water level. To see if this possibility existed a simple correlation analysis was performed comparing each independent variable with each dependent variable on a one to one basis (Table 10). Both estimates of insect damage were highly negatively correlated with plant height, leaf area index and leaves per plant. While this does not necessarily infer that a causal relationship exists between insect damage and the plant characteristics the possibility is present. Further more sophisticated analyses may be able to resolve this effect but the results of this study are inconclusive with regard to damage by insect damage.

The models produced seemed to fall into two broad categories, biomass and density. The first includes standing crop, plant height, leaf area index, and leaves per plant. These four characteristics are inter-related as evidenced by the significant positive correlations (Table 6) between them. Because of this interrelationship all are probably indices of biomass and all are low in the winter, increase in the spring, reach their peaks in early summer, and decline in the fall. All of them are primarily climatologically limited as evidenced from the inclusion of solar radiation and climate temperature in each multiple regression model (Table 7).

The major nutrients (N, P, K) are all included in at least one of the four above mentioned models. The coefficients for these are somewhat difficult to interpret. Nitrogen is included in the standing crop model.

**Table 10** Correlation coefficients ( $r$ ) between dependent and independent variables and predicted values for a greater  $r$

	Dependent Group	Plant PLOS	Leaf Area Index	Stems per Plant	Leaf Area Index	Plant PLOS
Order Reduction	0.708 (0.9400)	0.809 (0.8887)	0.764 (0.8887)	0.698 (0.9383)	0.898 (0.9913)	0.779 (0.9471)
Wet Air Temp	0.011 (0.9294)	-0.048 (0.9891)	0.180 (0.9887)	0.787 (0.8883)	0.394 (0.9433)	-0.028 (0.9883)
Wet Air Temp	0.129 (0.9244)	0.172 (0.9881)	0.512 (0.8887)	0.685 (0.8883)	0.075 (0.9913)	-0.189 (0.9891)
Wet W.D. Temp	0.130 (0.9874)	0.808 (0.8881)	0.585 (0.8887)	0.780 (0.8883)	-0.003 (0.9913)	-0.188 (0.9883)
Wet W.D. Temp	0.045 (0.9587)	0.179 (0.9887)	0.687 (0.9887)	0.738 (0.9887)	0.188 (0.9493)	-0.087 (0.9887)
Relative Humidity	-0.130 (0.944)	-0.188 (0.9881)	0.687 (0.8887)	0.673 (0.8883)	-0.071 (0.9913)	-0.188 (0.9881)
Leaf Group	-0.130 (0.9871)	-0.188 (0.944)	-0.081 (0.9881)	-0.087 (0.9883)	-0.075 (0.9874)	-0.188 (0.9883)
Proportion	0.130 (0.9881)	-0.188 (0.9881)	0.718 (0.944)	0.688 (0.9874)	0.188 (0.9881)	0.130 (0.9883)
Stemper	-0.081 (0.9871)	0.179 (0.9881)	-0.717 (0.9881)	-0.688 (0.9883)	0.080 (0.944)	0.718 (0.9874)
Time	0.045 (0.9883)	0.187 (0.9883)	-0.081 (0.9881)	0.130 (0.944)	0.188 (0.9881)	-0.081 (0.9881)
Constructing	-0.087 (0.9883)	0.188 (0.9883)	0.130 (0.944)	-0.081 (0.9881)	0.188 (0.9881)	0.188 (0.9883)
Performance	-0.087 (0.9883)	-0.188 (0.9883)	-0.130 (0.944)	-0.130 (0.944)	-0.188 (0.9881)	-0.188 (0.9883)
Regression	0.087 (0.9881)	0.188 (0.9883)	0.130 (0.944)	0.130 (0.944)	0.188 (0.9881)	-0.087 (0.9883)
Effect Size	-0.087 (0.9883)	0.188 (0.9883)	-0.130 (0.944)	0.188 (0.9883)	0.188 (0.9881)	0.188 (0.9883)
Wet	-0.087 (0.9883)	-0.188 (0.9883)	-0.130 (0.944)	-0.130 (0.944)	-0.188 (0.9881)	-0.188 (0.9883)
Leaf Length	0.087 (0.9883)	-0.188 (0.9883)	0.130 (0.944)	0.188 (0.9883)	0.188 (0.9881)	-0.087 (0.9883)

The step's correlation coefficient between standing crop and nitrogen (Table 10) is negative and not significant. After the effects of sun-light and water relations are removed into relationship is positive as is evidenced by the positive coefficient in the model. Since this shows that at constant levels of light and temperature the standing crop increases as nitrogen levels increase. However, since absorption of nutrients increases as standing crop increases one would expect a negative relationship between the two if nitrogen input from the various sources remains constant. This inverse relationship seems to be apparent in Figure 3 and 4a. The drop in nitrogen concentration in the water, however, is more likely due to an increase in the water level resulting in a dilution of the nutrient load. This is reflected by the significant correlation between nitrogen and lake level (Table 4). Mitsch (1974) demonstrated that a decrease in nitrogen across the marsh does occur and is greatest in the summer when the water/crop standing crop is high. Nitrogen, then, may very well be limiting to watercress/lotus and the increase supported by the available nutrients may increase as relative nitrogen concentrations increase.

Phosphorus is generally considered one of the primary limiting factors in aquatic systems (e. g. Howarth 1988). It is included in the model for plant height and the coefficient is negative. The simple correlation coefficient between phosphorus and height is also negative and significant. The model infers that with allomathic/plant effects removed, plant height increases as phosphorus decreases. This suggests an increasing absorption of phosphorus as the biomass increases. Phosphorus concentration, however, is also affected by the water level. High phosphorus concentrations are correlated with low water levels (Table 4). Mitsch (1974) showed a small

decrease in phosphate concentrations occurred across the month. In the summer, these plant growth probably does affect the phosphate concentration but it is difficult to determine if these concentrations increase relating to the plants. Monophosphate levels were 100% to the existing level of 0.18 mg/l as determined by the experiments of Heller et al. (1981) discussed earlier. The drop in phosphates may have been due to the absorption of luxury amounts by the plants beyond their immediate requirements.

Potassium was included in the plant height model after the effects of climate and phosphorus were removed. The simple correlation coefficient between height and potassium was negative and not significant (Table 10). The coefficient in the regression model (Table 1), however, was positive and significant. Potassium was also significantly correlated with water level (Table 4). The indication from the model is that at constant levels of sunlight, temperature, and phosphorus, plant height increases as potassium concentrations increase or vice versa. Again, one would expect the opposite, that is, as the plants become large absorptions would increase and the nutrient concentrations correspondingly decrease. The possibility exists that maximum nutrient absorption occurs early in the growing season. Nutrients may be absorbed in large quantities and stored within the plant. The period of maximum absorption may occur simultaneously with the period of fastest growth. As the growth rate slows nutrient absorption may also decrease. Hence, even though the plants are larger during the summer the plants may be having a lesser effect on nutrient levels. This may explain the apparent decline in potassium levels in March and April (Figure 7). This same explanation is also possible for nitrogen.

Other significant variables included in the four models which represent biomass are water level, pH, iron, and sulfates. The possible significance of water level and pH have already been discussed. Sulfates are correlated with magnesium, potassium, alkalinity, and conductivity. The inclusion of sulfates in the lowest per plant model may indirectly indicate the importance of sulfate salts. The inclusion of iron with a negative coefficient in the same model indicates the increased uptake of this essential nutrient as plant biomass increases. This agrees with my observations as plants grown in greenhouse cultures.

Leaf density and leaf density are highly correlated and form the second category. These two parameters, unlike the biomass indices, do not show a peak in the summer but rather in the spring. Potassium, iron, phosphorus, and water level were included in both models (Table 1). The signs for these coefficients are opposite those for the same variables in the previous models. The negative coefficients for potassium indicates that it is being absorbed as density increases. This supports the argument given above that potassium is absorbed in the greatest quantities at the time of fastest growth. Further, potassium is plants known to accumulate in those tissues that are growing rapidly (Robles et al., 1984) and would be expected to be absorbed in greater quantities when maximum growth occurs.

Iron, on the other hand, appears to be directly related to density. Although it is difficult to determine why iron concentrations showed a dramatic increase in the spring (Fig. 4) the strong correlation with plant density cannot be ignored. The iron-enriched water appears to have been at least partially responsible for the increase in density witnessed in the spring. Since iron is an important element for the synthesis of



chlorophyll) it may be an important limiting factor in the winter/spring seasonality.

Phosphorus was also directly related to leaf density and plant density. As leaf densities, therefore, rose when phosphorus concentrations are high, this is in contrast to plant height which achieves its maximum when phosphorus quantities are low. This may be interpreted as indicating that high phosphate concentrations early in the growing season are important in restricting the onset of rapid growth in the spring. As the plants become larger and biomass increases more phosphorus is absorbed and the concentration decreases.

Regression in the leaf density model had a negative coefficient. This may have reflected the uptake of nitrogen as leaf tissue increased. This would be expected since nitrogen is an important constituent of the chlorophyll molecule. This change is not shown in Figure 4, however.

Ecological variables did not appear to have the importance in the density models that they had in the biomass models. Solar radiation was included in the leaf density model but the coefficient was not significant. Maximum water temperature was considered the most important variable in the plant density model and was negatively related to it. This probably reflects inter-relationships of different characteristics within the plant population, however. That is, competition for light is reduced as the winter canopy allowing an increase in density. Once temperature is so important in the biomass model and biomass is inversely related to density.

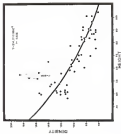
The multivariate analysis as presented does not take into consideration auto-regulatory features within the winter/spring population. The productivity studies show that small plants grow more rapidly than large

plants presumably because the large plants are closer to steady state with a smaller P.R. ratio. This is in spite of the fact that net efficiencies are approximately equal for both size classes. One would expect, then, that the plants would grow faster in the spring when the plants were small than in the summer when they were large even if external conditions were equal. This cannot be attributed entirely to an increased metabolic load in large plants because the gross primary productivity per gram of leaf tissue decreases as the plants become larger (see Table 6). This implies that a unit of large plant leaf tissue is less efficient than an equal unit of small plant leaf tissue. Respiration per gram likewise is almost double in the small plants so this cannot account for the difference. One possible reason for this difference is senescence of the older leaves. A second is intraspecific competition for light. Both of these explanations are probably partly true. As the leaves become older they gradually do become less efficient. Also they are more likely to have been attacked by diseases, often, insects, and other factors which may reduce their efficiencies. Also, as the plants become larger they are more prone to self shading. Hence, even though the amount of light received is the same as the small plants the amount received per unit of photosynthetic area would be inversely proportional to the degree of competition.

This pattern of self regulation by intraspecific competition seems to account for changes in plant density within the velvetleaf-rich community better than any of the physical parameters included in the plant density model. As shown earlier, small plant size classes are lost and plant density decreases as the plants become larger. Figure 2a further illustrates this. In this figure density is plotted as log function of plant height. This slightly improves the correlation coefficient derived

Figure 26

Plot density as a function of plant height. The greatest densities from the replicates (as averaged by date) during the 1961 season were obtained in the highest treatments. However, the mean value obtained did not differ



from the simple correlation in Table 1 ( $-0.406$  vs.  $-0.260$ ). Most of the data points fit the regression line extremely well. The greatest deviation from this occurs in April when a much higher density occurs than would have been expected based on plant height alone. Because density rapidly fell back to normal ranges I believe that this represents an "overshoot" response by the plants to favorable conditions. Early in the season constraints are high and competition for light is low. As a result the plants respond by producing a great number of offshoots. This numerical response greatly intensifies competition and as the canopy rapidly increases light is effectively cut off from the smaller plants resulting in their loss and a decrease in density. The surviving plants would be those that maintained their ability to reserve resources prior maturation. This would tend to increase in petiole length so that leaf display would be above the neighboring plants. Hence, in the summer a low density population of tall plants are present.

This phenomenon strikes me as very similar to a theory of forest cycles discussed by Whittington (1961) based on leaf caterpillar populations. He found that ecotone genetic viruses are present at low densities and tend to reproduce rapidly. Stagnant viruses are present in high densities and are adapted to crowded conditions. Conditions of low competition are present in a closed ecological community in the spring. In this situation the plant appears to be adapted to reproduce rapidly. During the summer under conditions of high competition the plants seem to be at stand-still and appear to be limited by environmental conditions. Like the leaf caterpillars they seem to be adapted to conditions of intense competition. Hence early in the season selection

favors those plants that can produce the most offspring earliest. Late in the season selection favors those plants that can compete for light most effectively. This results in the pattern of density observed in Figure 18. This explanation applies only to heterogametic populations which are limited by space not in the result of genetic flexibility within the population, rather than different genetic lineages. If open water continues to be available in the summer the reproductive phase may conclude with all available space is utilized as long as some other factor does not become limiting. This phase of reproduction is likely to occur only at the fringes of the wet, nearest the available space. The plants further back within the wet are more likely to be limited by competition for light and with generally no increasing in height. Considering that heterogametes are colonial species this pattern of growth is probably very adaptive. Increasing density in open areas enables the plant to colonize rapidly. It further increases the number of propagules available for reaching new disturbance areas to produce daughter colonies. Once the plants become established in an area their ability to compete must increase in order to maintain the colony. In its native habitat the ability to increase in height enables it to compete both intra- and interspecifically since several similar species occur with it (e.g. *Stuckermia acuta*, *Araceae* sp.). In the United States, however, there are relatively few large floating aquatic macrophytes and most interspecific competition is with plants in the littoral zone. In areas of deep water where emergent vegetation does not exist competition for light is intraspecific. Since relatively few herbivores act to reduce this intraspecific competition the population is limited only by climate and nutrients. Hence,

in Florida's wetland rich soils and moderate climate large stands of tall plants are common.

The pattern of growth of *Spartina patens* seems to involve several phases on Lake Alice. A period of 'no-growth' occurs in January and February when the standing crop begins to increase as increases in leaf density occurs. This begins as early as February and seems to be the first phase of growth. The leaf density peak occurs in late March. The second phase of growth is an increase in plant density. This begins in early March and the peak occurs in late April. The number of leaves per plant increases as leaf density begins its increase but levels off in March and April only to begin a new increase in May. The starting increase in leaf density is due both to an increase in the number of leaves per plant and an increase in plant density.

The third phase of growth is an increase in height which begins in late March and peaks in July. The increase begins when both leaf density and plant density are high and may be a response to this. Standing crop begins to increase at the same time as height and peaks at about the same time.

The fourth growth phase is an increase in leaf size and does not begin until May but reaches a peak in early July along with height and standing crop. Leaf production appears to be controlled first by an increase in leaf density, second by an increase in the number of leaves per plant, and finally by an increase in leaf size. The selective thinning seems to be that of maintaining leaf area under conditions of the competition this can best be achieved by producing more offshoots. Under conditions of intense competition each plant produces more leaves and the leaves increase in size. This may be interpreted as a diversion of

available energy in the path of an energy gradient. When the solar energy gradient is stronger peripherally lateral growth occurs. As peripheral light penetration diminishes due to increased competition and the light gradient becomes relatively stronger vertically, vertical growth begins to occur. Either way the increase in the leaf area index from early February through late May is almost continuous.

Finally, appears to show is the summer and a dramatic decrease in both leaf and plant density occurs. A summer decline in the number of leaves per plant, plant height and standing crop occurs in late July, August, and early September. The reasons for this are not apparent but it may be the result of a change in the carrying capacity of the system. These characteristics level off for a short while until a general decline begins in mid-September. This decline continues until the winter lows are reached in January. As plant height, leaf area, leaves per plant, and standing crop decline leaf density and plant density begin to increase. This increase continues until January when a slight decline occurs.

These annual cycles illustrate the flexibility of the waterhyacinth population in reacting to different situations. The population is regulated primarily by climatological factors, by water quality, and by the intensity of intraspecific competition. Rapid adjustment in the susceptibility of the net occurs as these factors change. It is not unreasonable to expect that this capacity to adjust may only be checked by insects. By reducing intraspecific competition insects may indirectly cause an increase in density. There probably is, of course, a damage threshold beyond which further damage by insects could severely affect the ability of the waterhyacinth population to adjust. I would expect this threshold to be high,



however, and to vary seasonally. I would expect the plants to be most vulnerable in the fall when solar energy is declining and the ability to store carbohydrates for winter survival is critical. By decreasing this ability the long-term effects of insect damage and freeze damage may retard the spring growth phase. Although freeze damage was highest in the fall it apparently was not severe enough to have any long-lasting effect on the waterpocketed community.

## CHAPTER II

### THE CONSEQUENCES OF STAGES OF AFFAIR WHICH MAY BE SOME ECOLOGICAL CHARACTERISTICS AND MORPHOLOGICAL FEATURES OF SPREADING

#### Introduction

The effects of an insect attack on a host plant depends not only on the biology of the insect but also on the ecological response of the plant. Harris (1942) noted that insect attacks may decrease plant abundance, have no effect on plant abundance, or actually stimulate plant growth. He further stated that insects which feed on specific plants may cause uprooting of the stems from which propagation occurs and increase the spread of the plant. Bennett (in Harris 1942, apparently referring to Vogel and Oliver (1936)) stated that it has been demonstrated that a large noctuid (probably *Prodenia*) which attacks *Salicophila* (*Prodenia* *salicophila*) may cause more plants and spread the seed. Vogel and Oliver (1936) attributed this increase in the number of plants with increasing insect concentrations to a reduction in defoliation of the apical bud. Their hypothesis was that by feeding on the apical meristem the insect caused the expression of the lateral buds thereby increasing the number of axillary branches.

If herbivory can cause the spread of a weed and thus increase the problem, it is imperative to determine the mechanism by which this occurs. A number of explanations other than a reduction in apical dominance are possible for this increase in effects. A reduction in intraspecific competition or an increase in seedlings due to an accelerated turnover rate may contribute to this. Several effects must also be considered. The purpose of this study is to explore in detail the

potential effect of stream flows on the ecology of the macroinvertebrate fauna in terms of net productivity, standing crop, turnover rates, and other characteristics of the plant community during two distinct seasons (summer and fall).

### Methods and Materials

The sides of four greenhouse tables 12 inches deep were constructed from 1 inch by 10 inch boards. The tables were lined with 4 mil polyethylene sheeting and filled with water. The water on all tables was fertilized equally, as needed, with 20-20-20 water soluble commercial plant fertilizer with minor elements. Inexpensive iron was also added to obtain concentrations of 2.5 ppm. Square foot grids were constructed on each table by stretching nylon fabric across the top of the tables and tying it off on nails spaced one foot apart. The tables provided 20 one sq. ft. quadrats each and two of the tables which were connected together provided 42 quadrats each. One small waterhyacinth plant in the inflated petiole stage taken from Lake Alton was placed within each quadrat in all tables and the plants were allowed to grow for several weeks until the tables were completely covered. Five quadrats were then randomly selected from each table and the plants were harvested to obtain basic measurements for the parameters to be evaluated. In the first experiment average plant height, no. leaves/quadrat, no. of leaves/plant, and no. plants/quadrat were counted and to obtain initial biomass estimates for the table. The same variables were estimated in the second experiment in addition to total dry weight subdivided into living and dead organic material. The living material was further subdivided into leaves, rhizomes, roots, and stolons. Where applicable these measurements were related to some of both unit area and fertilized plant.

Drone house eggs were collected for the first experiment from pickeral weed (*Potamogeton nodosus*) at a lake near Palmar deli, Florida, on 26 June 1964. These were allowed to hatch and neonates were placed on the tables in sufficient numbers to achieve 5, 8, 12, 16, 20, and 24

terns/plant levels of infestation. Five quadrats were again selected on 15 July and again on 2 August 1984 and the same parameters measured. Also the no. of larvae damaged, no. mines damaged, severity of the damage, no. larvae, no. pupae, no. pupal casts, no. dead larvae, apparent location of each larva, etc. was determined. Final values were taken on two separate dates (when the larvae were approximately 30 and 35 days old) so as to bracket the damage activity. Underestimation of damage would be obtained if the plants were harvested before the insects reached full size or after they ceased feeding and the plants had begun to recover. For this reason, it was desirable to harvest the plants at the time when the insects had begun to pupate. The final values are therefore expressed as the mean of two quadrats taken five at a time on two separate occasions. To further standardize the results the final values are expressed as a percent of the initial value  $\text{L.N.} = \frac{\text{Final}}{\text{Initial}} \times 100$ .

The eggs for the second experiment were the  $F_2$  generation of the larvae from the first experiment and were collected from waterpocketing. Initial samples were taken 1 October 1984 and the replicates were taken about 2 October. The levels of infestation were the same as in the first experiment. This experiment was allowed to proceed somewhat longer until 14 and 18 November (42 to 52 days). Other than the increased duration and the greater number of parameters measured this experiment was like the first one.

### Analysis

After determining that there was no significant difference (Student's *t*-test for unequal data) in any of the parameters measured between the two post-infestation sets of data they were combined to obtain 30 observations per treatment level for each parameter after the generation of insect activity. The final results are expressed as the mean values of 30 percentual final values for each level of infestation and are expressed as a percentage of the initial value.

The results were interpreted by means of the regression procedure from the Statistical Analysis System in the University of Florida IBM 360 computer. The results were fitted according to the three following regression models where *Y* = plant response and *X* = insect concentration:

$$1. \quad Y = A + BX$$

$$2. \quad Y = A + BX + CX^2$$

$$3. \quad Y = A + BX + CX^2 + DX^3$$

$$4. \quad Y = A \cdot e^{BX}$$

The model which best fitted the data and presented a realistic estimate of response trends was selected for plotting. The best fit to the first three models was determined by examination of the sequential sum of squares. The fourth model was compared with the others by means of the regression coefficients (*r*<sup>2</sup>). The model with the largest *r* was selected only if it was a great deal larger than the alternative model. Otherwise the model most clearly representing the results in the simplest form possible was chosen. In the majority of the cases the simple linear model (equation 1) provided a satisfactory representation of the results. It was originally expected that the data would conform to the log concentration model (eq. 4) but this regression consistently provided a lower *r*-value

than the linear model. Because of this and because the log model produced predicted values lower in particular means which underestimated the ortho-*optix* mean this model was never selected. If a greater number of higher levels of insect infestation were used in the experiment I believe the exponential nature of the response curves may have become more evident. Even though the regressions in this paper are linear the true relationship between the plant response and the insect concentration may not be linear.

## Steady State

### Plant Height

As autotrophic stands become denser they become shaded less intensely and instead of producing more shade they increase in height. As the plants become taller the biomass increases exponentially as is illustrated in Figure 27. As the living tissue increases the respiratory demand must also increase. Due to crowding and intraspecific competition for light the amount of photosynthetic tissue needed to maintain the plant must also increase. The ultimate result is that the productivity/respiration ( $P/R$ ) ratio decreases with  $H$  approaches 1 (Green et al., 1984). This steady-state is achieved when the energy produced is just sufficient to meet the respiratory demand of the plant and net production approaches zero. The standing crop at steady-state depends upon the carrying capacity of the habitat. A substrate-rich body of water supports a larger steady-state standing crop than a nutrient poor body of water. As long as substrates are continually replenished and solar energy remains high a steady-state equilibrium will be maintained. Density and biomass become balanced with respect to their demand of energy unless other factors intervene to disrupt this stability. Because plant height is related to stand density as well as the plant weight it also reflects internal density. Since the taller leaves (from which I measured height) are older, they are more prone to insect attack due to an increased duration of exposure. Height, then should be a very sensitive index of feeding activity by herbivores. Feeding either disrupts steady state.



Figure B2 Average dry weight per waterhyacinth plant as a log function of the average height.

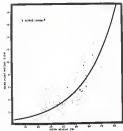
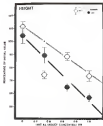


Figure 28 represents the response curve for plant height to one generation of feeding by *Aonema* larvae with varying initial larval concentrations in the summer and in the fall. At the time the plants were infested the stands had approached a steady-state as reflected by the small increase in the controls (10% and 5% respectively). As feeding intensity increased a nearly linear decline in both experiments was observed. The 0.25 level of infestation appeared to be slightly too in the summer experiment but this was the consequence of a severe attack by spider mites (*Chromaphysa pluvialis* Davis) which occurred on that date. A somewhat greater response to herbivore activity was observed in the fall than in the summer. This is as expected and appears to be due to an interaction effect between decreased solar radiation in the fall and herbivore activity.

Figure 24 The average height per waterhyacinth plant has increased from the highest level as a function of the feeding activity of *Arauca obesa* larvae. The mean represented data taken after a generation of feeding attack expressed as a percentage of the mean values for the same variables taken before the insects were introduced. The circles represent the mean values taken from ten 5.0L 100 water samples. The brackets enclose the range of the standard error of the mean. The open circles (dotted line) are values from the summer. The solid circles (solid line) are values from the fall. The summer data for the 5.00 insect concentration was excluded from the regression analysis because of the effects of a heavy spider mite infestation.

$$\text{Summer } Y = 170.43 + 36.23X, r = -0.8045$$

$$\text{Fall } Y = 103.92 + 46.13X, r = -0.8146$$



### Leaves

The terminology of vascularized leaves is an area of controversy among botanists. In general there are two distinct portions, the more or less swollen base and the blade. According to Jensen (cited in Kaufman and Corle, 1968) the blade is not a true lamina but an extension of the petiole hence it is often referred to as a pseudo-lamina. For the purpose of this discussion I will refer to the swollen base as the petiole and to the pseudo-lamina as the leaf blade.

In open stands the petioles are inflated containing numerous air spaces and function as floats and, as mentioned previously, tend to be short. In dense stands, however, the petioles are elongate and tend to lack the inflated float depending instead on the support of the dense neighboring stems and the interlocking of adjacent plants to hold them erect.

Since *A. desus* feeds on the leaves as well as the rhizome the effects of feeding activity should be reflected in a leaf number response (Figs. 15 & 16). By killing the plant a decrease in leaves/leaf area should be observable when plant density also decreases. Since plant density responses vary (Figure 11) the number of leaves per unit area will not always reflect insect activity. A better index appears to be leaves per plant. As the insect feeds on the leaves the number per plant should decline. Likewise, if new offshoots are produced they would tend to be smaller and have fewer leaves than their parent plants. Figure 25 illustrates the response curves of leaves per plant to varying insect concentrations in the summer and the fall. With the exception of the controls the means were almost identical in both experiments. The difference in the controls is probably due to a seasonal effect as explained earlier.

Figure 28 The effects of varying levels of insect feeding activity on the average number of larvae per waterhyacinth plant, expressed as a percentage of predevelopment mass. Legend as in Figure 25.

Control:  $P = 100.18 \pm 40.830$ ,  $r = +0.76$

FA11:  $P = 712.20 \pm 53.698$ ,  $r = +0.89$

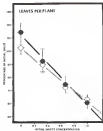




Figure 26: The effects of varying levels of insect feeding activity on the total number of waterhyacinth leaves per unit area expressed as a percentage of predefoliated areas. Legend as in Figure 25.

$$\text{Summer: } Y = 126.31 + 1.72X, r = 0.802$$

$$\text{Fall: } Y = 134.28 + 04.54X, r = -0.532$$

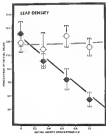


Figure 20 illustrates the response curves in terms of leaves/unit area. The changes in this measurement were quite different between the two seasons. In the fall the percentage of the total number of leaves present showed a significant decline with increasing insect concentrations. During the summer, however, no change was apparent. Since a decrease in the number of leaves per plant was evident with stability in the leaves per unit area was apparently due to the increase in plants.

### Plant density

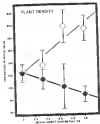
When discussing the effects of stress on the density of waterhyacinth (number per unit area) one must be careful to define the seasonal stage of the plant and the type of stress it is growing in. Waterhyacinth requires abundant solar energy, waters rich in nutrients, and open space for maximum productivity (see the discussion in the seasonal ecology of this plant presented earlier). Root factors which are likely to stress waterhyacinth (such as hemichides, frost, or insects) tend to open up the canopy. The plants become smaller and as a result the R/S ratio and net efficiency probably increases (Breed et al. 1984). In this situation they become r-strategists and reproduce rapidly competing successfully with other species for the available space. This is observed in the spring when there is an apparent "overshoot" in the plant population. The data from experiments with laser beams for the control of this plant illustrates the same principle (Jung and Smith 1983). After the laser treatment a decline in the rate of change was observed but it was immediately followed by a sharp increase until the experimental plots were almost identical to the control plots.

In this r-selective situation species with high rates of reproduction and growth are more likely to survive in an unstressed situation (J. P. Oden, 1983). When the waterhyacinth stand matures and occupies the total available space an equilibrium density is reached. In this situation the plants appear to be K-strategists where selection favors species with lower growth potential but which are more competitive under equilibrium densities (J. P. Oden, 1983). The effect of the insect (or other stress factors) appears to be that of causing the plant to "revert" strategies by disturbing the equilibrium density. Disturbance of the stress

Figure 3b The effects of varying levels of roach feeding activity on the number of antispinulosis plants per unit area expressed as a percentage of predefoliated mean. Legend as in Figure 3a

$$\text{Summer: } Y = 138.77 + 31.37X, \quad r = 0.4959$$

$$\text{Fall: } Y = 123.85 - 35.53X, \quad r = -0.3758$$



would allow the equilibrium density to again be reduced and the available space occupied according to the carrying capacity of the habitat.

If these assumptions are true, then one would expect the seasonal consequences of insect attack to vary. The carrying capacity of the habitat depends to a large extent on water stress. In the summer when water stress is nearly maximal one would expect insect infestation to ultimately result in an increase in the absolute density of the plant since energy is high and space is available. In the late fall, when water stress is easing, these consequences may be much different because of the reduced energy available the carrying capacity is reduced. An increase in available space at this time may ultimately result in little change or a decrease in plant density as other factors (i.e. water energy) become limiting. The data from this experiment (Figure II) tends to support this hypothesis. If insect damage to the vertical bud was solely responsible for these increases in density without the influence of other factors, then it would be reasonable to expect the plants to react similarly in both experiments. Instead I observed an increase in density in the summer experiment and a slight decrease in the fall experiment which favors the seasonal interaction explanation for density changes.

I do not intend to dispute the fact that damage to the terminal bud may cause a response in the direction of internal growth. One could cite many examples of similar phenomena in very different plants. From field observations, however, it is worth noting that the effluents produced from plants with severe damage from a *A. down* do not appear to be as vigorous as normal effluents. These effluents are often deformed and the leaves often appear to be rather thick and leathery. I merely intend to demonstrate that the evolutionary strategy of the plant is to produce

effects when sufficient space and water energy is available. This occurs with or without an interaction of insect attack. From a biological control standpoint the fact remains, whatever the cause, that an increased number of plants may be tolerated and the possibility of suppressing the spread of this plant does exist. I contend that the activity of the weevil does not influence spread. Spread occurs primarily by the small floating plants which grow peripherally from a stand of larger plants toward the open water. The limiting factor is space, if space is available insects can do no harm. If space is available the plants will grow into it unless growing conditions are suitable. If the total area available is completely occupied by waterhyacinths the density of the plant population is inconsequential. The only undesirable effect that may be the result of insect activity is that of fragmenting the stand causing daughter colonies to float off more frequently and become established in new areas. It will be discussed subsequently, other parameters often make more fully the true impact of a given feeding activity on waterhyacinths. Because of differences in the growth pattern of the plant, density is not a good index of herbivore effectiveness.



### Biomass Estimates

The effect of varying insect concentrations on the total biomass per unit area is shown in Figure 33. Total biomass, as defined here, includes a living component (standing crop) and a non-living component (detritus), Figures 33 and 34, 1 & 2, the total organic material present. Biomass estimates were only taken in the fall experiment, therefore summer experiments cannot be considered. The summer standing crop (Fig. 33) could be estimated, however, using predicted values from the regression equation in Figure 27 for average weights per plant multiplied by the number of plants per unit area. The value for standing crop at the 0.10 level of infestation was corrected for silk damage by interpolating the expected values for height and plant density from Figure 1a and 1b assuming approximate linearity between the 0 and 0.02 levels of infestation.

Total biomass (Figure 33) revealed a rather unexpected response to insect concentration. At all four levels of infestation no biomass was evident. The control (0 infestation level) increased 10%. The plots treated with insects, however, responded very similarly at all three levels of infestation resulting in approximately a 30% increase over the control biomass present. The effects of insects on total biomass was not significant.

The standing crop (gross living material per unit area) declined significantly with increased initial insect concentrations in the fall experiment. If it is assumed that the estimated regression for the standing crop values in the summer experiment is reasonably correct a quite different response is apparent. Instead of a rapid decline seen with low infestation levels no response is apparent until the infestation

Figure 32. The effects of varying insect concentrations on the initial water-soluble biomass (expressed as both detritus and living plant material). Data was taken only from the Fall experiment. Legend as in Figure 29.

$$\text{Regression: } Y = 180.75 + 26.44X, r^2 = -0.988$$

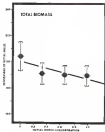


Figure 10. The effects of varying insect concentrations on the living *Salicaphysalis* mass present per unit area. Data was only taken from the full experiment, however, estimates were made by calculating the average weight per plant from Figure 21 (used as the average plant height and multiplied by the plant density (open circles and dotted line). The summer curve was fitted by eye. Otherwise, legend as in Figure 12.

$$\text{Regression (Full)}: Y = 145.95 + 122.71X, r = -0.6624$$

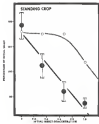
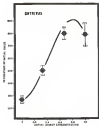


Figure 34. The effects of varying insect-feeding activity on the amount of dead interweave/leaf plant material (g/section) per unit area. Data not taken only from the full experiment. Legend as in Figure 29.

Regression:  $\hat{Y} = -0.09(16) + 0.780X = -1.44 \text{ Std } Y +$   
 $-0.0002 \text{ Std } X^2$ ,  $r^2 = -0.3794$



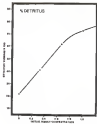
reaches the 1.00 level. This probably reflects the carrying capacity of the plant community for this herbivore. The carrying capacity is probably dependent upon the initial standing crop as well as the productivity of the plant, i.e., the rate at which the community can replace itself. The plants in the summer are more productive than those in the fall and, as a result, can support a greater herbivore population. The point at which the herbivores begin to have a negative effect on yield is the response threshold. In the fall this threshold occurs between the 0 and 0.25 levels. In the summer, however, the threshold apparently is much higher at between the 0.47 and 1.00 levels of infestation.

The change in the amount of detritus (dead organic material) present is probably a good indicator of insect feeding activity provided that it can be collected accurately and identified as waterlogged detritus. The net change is dependent upon the living material available during the period of infestation, the level of insect feeding activity, and the rate of degradation of the detritus by decomposers. Assuming that the decomposition rate per gram detritus is constant the amount of dead organic material should directly indicate insect feeding activity up to the point where it becomes limited by the amount of living material available for conversion. A detrital response curve regressed on insect concentration (Figure 2C) would be expected to increase up to a point, tend to level off, then show a rapid decline. The point of deflection for this curve should occur at the point where plant productivity begins to be reduced by the feeding activity of the insects. As insect concentrations become larger (beyond the range of this experiment) this point would be reached earlier in the growing period of the plant and cause a decline in the



curve until it levels off at a point where the increase in detritus is equal to the initial living material present. Figure 26 illustrates this somewhat differently as an almost linear relationship between the insect concentration and the amount of detritus present expressed as a percentage of the total organic material present. This linear relationship should hold until the ratio of detritus to biomass approaches unity. At this point an asymptote in the curve should become apparent where higher concentrations of insects have a proportionately smaller effect on this ratio (a ratio of greater than 1.0 is impossible). If the net productivity is zero and the detritus : total biomass ratio is 1.00 then all of the plants were immediately killed upon release of the insects. If this ratio is 1.00 and the net productivity is some value greater than zero then all of the plants were killed at some time after the initial release.

Figure 35. Debris as a percentage of total sediment in Herring as a function of beach feeding activity. Curve fitted by eye



### Productivity and Turnover Ratios

The relationship between biomass and detritus can be more graphically illustrated if net productivity and turnover rates are considered (Figs. 36 and 37). Net productivity, as used here, is defined as the final quantity of organic material present (total biomass present at the end of the experiment - detritus present at the beginning) per quantity of living material initially present and is expressed as a percentage. A value of 100 for net productivity would indicate no change in biomass and is the original value possible. Statistically Figure 36 indicates that there was no significant change in net productivity as a result of insect feeding activity. Intuitively there does appear to be some effect, however, as productivity was approximately 120% at all levels of infestation whereas it was approximately 28% for the control.

Knowing that productivity was not affected by the insect population and with the knowledge that standing crop was significantly reduced, it can be deduced that the important function of the insects was that of accelerating turnover. The effects of insect feeding activity on the relative turnover ratio is illustrated in Figure 37. The turnover ratio as used here refers to the change in detritus per unit area per gram of living plant material initially present. It is inversely related to turnover time or the time required for the initial living material to be converted to detritus. An approximately linear relationship is apparent between insect activity and the turnover ratios. The ratio translates into a range of turnover times of approximately 160 days for the control to 40 days for the 1:10 infestation level (where  $\text{turnover time} = \frac{1}{\text{turnover ratio}} \times 40 \text{ days}$  (mean duration)). It is obvious, then, that the turnover time decreases exponentially with increasing insect concentration. These

Figure 25. Net enteric/whole protection as a function of faecal feeding activity. Net production, as used here, refers to the final quantity of organic matter present, excluding the initial amount of detritus, as a percentage of the initial living plant material. Data only from the full experiment. Legend as in Figure 20.

$$\text{Regression: } Y = 794.42 - 27.59X, r^2 = 0.799$$

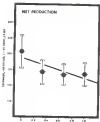
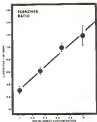


Figure 17 The ratio of conversion of living unseparated plant material into detritus as a function of mean feeding activity. The figures are based on the change in detritus over one generation of drosophila population divided by the amount of conversion of living material present at the time the insects were introduced. Data only from the full experiment. Legend as in Figure 2b.

$$\text{Regression: } Y = 0.1254 + 0.0029X, r = -0.1125$$





relationships should remain fairly constant regardless of season since they consider only total living material present and detritus produced

### Plant Parts and Proportions

The response curves for the weights of various plant parts to varying levels of insect infestations show very similar trends and tend towards exponential declines (Figures 26-32). Regression analysis, however, showed that the log response curves did not improve the correlation coefficients when compared to a linear response curve. The results, therefore, are plotted as straight line relationships. If further data were available beyond the levels of infestation tested in this experiment a curvilinear response might be more evident.

Of the four plant parts rhizomes showed the greatest increase in the control treatment at approximately 20% of the initial value. The 0.10, 0.47, and 1.00 levels showed responses of 20%, 40%, and 60% respectively. This indicates that in a situation without an insect infestation and greatest proportion of the carbon fixed is stored in the rhizome. The proportion of rhizome weight to total living plant weight tends to support this. The rhizome represented 8.3% of the initial plant weight and increased to 11.6%, this represents an increase of 40% (see Table II). Bechman and Karle (1968) stated that the rhizome was the main organ of storage. It is apparent in this study that a great deal of the energy assimilated by the plant is stored in the rhizome as carbohydrates. Insects, by causing a decrease in the ability of the plant to create this storage, cause a depletion in the carbohydrate reserves. This directly affects the ability of the plants to survive periods of further stress and to recover from the rhizome if the leaves are killed. This may reduce the ability of the plant to survive periods of cold, herbicide treatments, pathogens, and further insect attacks.

**Figure 38** The effects of varying insect feeding activity on waterhyacinth stem mass (greenhouse-bias and petioles). Data only from the field experiment (logged as in Figure 38).

$$\text{Regression: } Y = 13.127 - 129.89X, r = -0.4501$$

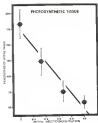


Figure 26: The effects of varying insect feeding activity on waterpotential micro-plant mass (roots, rhizomes, and shoots). Data only from the FvTi experiment. Legend as in Figure 25

$$\text{Regression: } y = 121.94 + 109.68x, \quad r = -0.6349$$

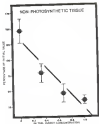


Figure 32 The effects of varying insect feeding activity on whitefly/lettuce root mass per unit area. Data only from last experiment. Legend as in Figure 26.

Regression:  $Y = 86.19 - 23.09X$ ,  $r^2 = 0.640$

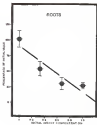




Figure 4) The effects of varying locust feeding activity on the waterloggedness-induced mass protest per unit area. Data only from the full experiment. Legend as in Figure 2)

$$\text{Regression: } \hat{y} = 0.074x_1 - 149.21x_2, r = -0.4962$$

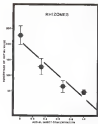


Figure 40: The effects of varying brood feeding activity on the watergap:old mass represented as scales per unit area (data only from the full experiment). Legend is in Figure 39.

$$\text{Regression: } Y = 1.61 X - 17.382, r = -0.9118$$

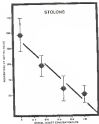


Table 11. Action of the various plant parts and the percent change in the final values as compared to the initial values. The simple correlation coefficient ( $r$ ) is derived from a linear regression analysis.

		Insect Concentration				$r$
		0	0.33	0.67	1.00	
Leaf Wt. Plant Wt.	Initial	0.771	0.704	0.735	0.804	-0.172 <sup>†</sup>
	Final	0.706	0.768	0.837	0.793	0.219 <sup>†</sup>
	%	70.82	77.13	77.22	77.47	-0.250 <sup>†</sup>
Stem Wt. Plant Wt.	Initial	0.807	0.893	0.890	0.879	-0.199 <sup>†</sup>
	Final	0.716	0.889	0.878	0.879	-0.088 <sup>††</sup>
	%	73.23	90.64	88.76	89.80	-0.433 <sup>††</sup>
Root Wt. Plant Wt.	Initial	0.148	0.135	0.136	0.132	0.040 <sup>†</sup>
	Final	0.076	0.092	0.090	0.091	0.025 <sup>†</sup>
	%	60.48	48.37	47.49	62.91	-0.739 <sup>†</sup>
Stem Wt. Leaf Wt.	Initial	0.029	0.027	0.026	0.026	0.395 <sup>†</sup>
	Final	0.029	0.028	0.023	0.023	0.142 <sup>†</sup>
	%	71.43	105.18	65.71	75.47	-0.073 <sup>†</sup>
Root Wt. Leaf Wt.	Initial	0.026	0.026	0.027	0.025	0.064 <sup>†</sup>
	Final	0.017	0.024	0.024	0.026	-0.380 <sup>††</sup>
	%	65.38	97.98	92.48	96.92	-0.550 <sup>††</sup>

<sup>†</sup> Probability ( $\alpha$ ) of a greater  $|r|$  is 0.05; <sup>††</sup>  $\alpha=0.01$ ; <sup>†††</sup>  $\alpha=0.01$ .

The quantity of carbohydrates available for storage is related to the amount of photosynthetic material present to produce it and the efficiency of the plant. The effect of reducing the amount of leaf tissue as a result of insect feeding would be that of reducing the energy available for storage or maintenance. Except for the controls, leaf tissue changes (Fig. 36) closely paralleled the changes in rhizome tissue at 1200, 700, and 520 for the 0.33, 0.47, and 1.00 infestation levels. The control plant leaf weight was 18.5 of the initial weight. Hence, insect feeding directly reduced the photosynthetic tissue present and directly or indirectly reduced the material stored as rhizome tissue.

The proportion of the living plant weight represented as green mass increased in the controls from 8.7% to 9.7% or approximately 10%. This figure was somewhat greater in the plots treated with insects (see Table II) but does not appear to be linearly related to insect concentration. This increase in proportion was probably due to a decrease in the non-photosynthetic tissue.

The non-photosynthetic tissue (Fig. 36) not only increased less in the control treatment (ca. 50%) than photosynthetic tissue (ca. 100%) but also decreased more in the insect treatments. This resulted in a decrease in the root-rhizome shoot ratio (Table II) at all treatment levels. This ratio decreased less in the control plots (55% of initial) than in the treated plots (33-55). Again, this does not appear to be a linear relationship. This does indicate, however, that the effect of insect activity decreased the stored material (rhizome) as well as the ability of the plant to absorb nutrients relative to the photosynthetic ability of the plant.

While nitrogen weight increased the most in the controls, roots represented the least (Figure 4b) or more accurately did not increase (200). This agrees with field observations where I have found that small water-hyacinth plants have nearly the same root mass as 10 large plants when growing in similar conditions. When the plants are small crowding is abundant and nutrients would be more limiting than light. The plants, therefore, probably maintain root growth early in their growing period. As the plants grow and light becomes more limiting due to intraspecific competition the available energy is probably shifted more towards shoot development and less towards root development. This would explain the decrease in the proportion of the plants represented as roots and the decrease in the root:rhizome shoot ratio observed in the controls in Table II.

Roots increased the least in the control and decreased the most in the treated plants (20) of initial values with 1.00 (mass per plant). Values for final proportions ranged between 41 and 136 of the initial proportions after insect feeding. This is not significantly different than the control (200). Because shading by adjacent plants is reduced and increased amount of light is available for growth. For optimum regeneration of the plant, nutrients need to be absorbed readily for the full photosynthetic potential to be realized. Ideally, then, the proportion of the plants represented as roots should become larger as is generally the case in small plants. The root proportion does not change as a result of insect attack, therefore regeneration of damaged plants is probably slower than would be expected. Because light energy and nutrient energy react motivationally in plant production the availability of one affects the utilization of the other (i.e., growth is

limited by the accessory resources which in forest are limited). When light energy is abundant, as in a sparsely populated stand, nutrient levels probably limit growth. One would expect the response of the plants in this situation to be that of maximizing root development thereby increasing nutrient absorption and minimizing the limiting effect of nutrients. In a dense stand where intraspecific competition for light is intense light availability would be expected to be limiting. In this situation selection would favor those plants with maximum photosynthetic tissue and the tissues necessary for photosynthesis display. Hence, a greater proportion of the available energy would be expected to be utilized in producing photosynthetic tissue. Small plants, therefore, would be expected to have a larger root-rhizome shoot ratio than large plants. The effect of the insects in this experiment resulted in smaller plants but the root-rhizome shoot ratio did not become larger than that of the large plants in the control (it in fact was generally smaller). As a result the available light increased but the plants could probably not efficiently utilize this increase because of the limiting effect of the absorptive ability of the small root mass. Small slowly growing plants were produced as a result instead of small rapidly growing plants or large slowly growing plants. The insects caused not only a decrease in the standing crop but probably also inhibited the natural regenerative ability of the plants remaining.

The crown weight decreased directly as a result of insect activity (Figure 42). Crown weight as a proportion of plant weight should reflect offset production. If the effect of the insects was that of increasing the offsets produced then the crown weight and the crown weight-plant weight (crown:plant weight) should increase. This did not



appear to be true in this experiment. The radish:plant weight ratio (Table II) was not significantly different between the infestation levels tested. This agrees with the plant density changes discussed earlier.

### Discussion

It is evident from these two experiments that a seasonal effect interacts with insect activity and produces varying plant responses depending upon the time the infestation occurs. The assumption that insects directly cause an increase in plant density appears to be oversimplified. The stress is reduced as it is reduced by reduction in both light and photosynthetic material. This effect is increased penetration of available light and air accelerate the growth of the remaining plants. This may be due to a cessation of rather than a direct result of stress. Any stress factor that would reduce the effect of intraspecific shading by reducing the canopy would probably result in a short term increase in the number of plants present until a new equilibrium density is achieved. Competition may become increasingly important and suppress this density increase by interspecific competition in the field. In these greenhouse experiments competing species were not present so this response may be exaggerated.

The effect of insect damage to the terminal bud could possibly contribute to an increase in the number of plants. I feel that the contribution by insects to this process is minimal. Penfold and Earl (1944) found that aspartate ribonase failed to produce new sprouts only when 4 cm of the ribonase tip was removed. The ribonase of the majority of the plants were thoroughly fringed as a result of attack by the larger larvae and the plants were dead. Fewer than 10% of the surviving plants had ribonase damage. Those with ribonase damage produced either stinky offshoots. The offshoots remaining after insect attack were not the type that usually occur in open stands. The petioles were not hollowed so as to function as flutes as their ability to disperse

is doubtful. Thus, the root mass and the root:shoot:shoot ratio was small indicating a loss of efficiency. The increase in plants in the summer is more likely a vegetative response of the surviving plants before they are severely damaged by the increased space available. In this manner the canopy maintains a larger standing crop and supports a larger insect concentration before yield is affected.

Survival over periods of stress, such as winter freezing, would probably be reduced by insect infestations. Redwood and Davis (1940) stated that as the leaves are killed by frost the plant turns to frost water increasing the susceptibility of the rhizome to frost. Insects have the same effect of removing water and causing the rhizome to become more exposed to temperature extremes. Further, the ability of the plant to regenerate after periods of stress is probably decreased as a result of insect attack because of a depletion of carbohydrate reserves in the rhizome.

Surprisingly, productivity did not decrease significantly as a result of insect attack. This is probably the result of a time factor. That is, the insects failed to produce a noticeable effect on plant growth until they reached a stage late in their development. Only the later instars do severe damage to the rhizome. Once this point was reached productivity probably was reduced but it occurred so late in the experiment that it failed to show up in the results. This same phenomenon was apparent in the total biomass estimates. The only factors that did not show a significant response to insect attack were net production, total biomass, and plant density.

All factors associated with the standing crop showed a highly significant decrease as insect concentrations increased. The proportions of the various parts of the plants changed but these changes, for the

most part, were not out of line with those of the controls. This was surprising because the weather plants produced were expected to be taller in the plants growing in open stands (i.e., a high root:shoot ratio). This did not appear to be true.

The turnover ratio was the next revealing characteristic measured. Living material was killed and transformed to detritus at rates almost directly proportional to the insect concentrations. The total amount of living material initially present survived approximately 35% as long with 2 larvae per plant as did the plants without insects. This accelerated turnover could severely affect the competitive ability of the plants.

In summary, *Arum dasycarpum* severely affected almost all aspects of waterhyacinth growth. It does appear to be a good agent for biological control and mass releases should be attempted. The chances for success would be greater in the fall than in the summer and I believe concern over a resultant increase in plant density and dispersal is unwarranted. The major problem with this insect is that parasite heliids tend to cause pollen in the efforts of *A. dasycarpum* and as noted previously waterhyacinth recovers rapidly after cessation of stress factors. Insects which are not limited by parasites and exert continuous pressure on the plant community will probably have a greater long term possibility of providing a permanent control. Releases of *A. dasycarpum* may be beneficial in conjunction with studies to bring the plant population down to levels more easily controlled by the host(s).

THE FEASIBILITY OF THE UTILIZATION OF *Arctostaphylos uva-ursi* FOR  
THE BIOLOGICAL CONTROL OF WATERMELON - THE EFFECTS  
OF AN INTRODUCED POPULATION ON A SMALL FOWL COMMUNITY

### Introduction

It has been suggested that *Arctostaphylos uva-ursi* could be used for the biological control of watermelons *Citrullus melanosperma* (Purt. & Schum.) by supplementing natural populations if a satisfactory method of mass-rearing was developed (Vogel and Oliver 1966). Tract (1964) also suggested the possibility of supplementing populations of native insects to increase their effectiveness in weed control. While this tactic has been discussed by various investigators in the field of biological control there are few examples of studies where this has been attempted in an effort to control weeds.

Sufficient numbers of *A. uva-ursi* were reared on living watermeloned plants in a greenhouse to release for a small scale field test. Three variables were important in the location and timing of this release. First, the site had to be small to achieve an adequate insect-plant concentration. Second, the release had to be synchronized at a time when parasite populations were low and the natural *A. uva-ursi* population was increasing. Third, the release had to be strategically made so as to disrupt the plants at a time when they were most vulnerable to attack. While this criteria limited a small site near Eugene, Oregon in Alameda Co., was selected where the previous summer the largest killing of the natural *A. uva-ursi* population occurred in the late summer and fall. Also, an attack late in the growing season of the plants should increase

their susceptibility to winter cold and increase their chances of surviving until spring. Hence, the releases were made in mid-August and adequate time for two or three generations before evaluating the effects of the release.

I had two strategies in mind to achieve the desired results with the initial release. The first was that of predator satiation (see Lloyd and Dyke 1964; Jensen 1969) where a sufficient number of larvae had to be released to satiate the predators and parasites present thus paralyzing an adequate number to escape. The larvae also had to be of a uniform age class so as to carry this phenomenon through to affect all age-specific parasites. Age parasites were avoided by allowing the eggs to hatch prior to release. An introduced parasite (*tracheatus* sp.) is present in low populations in the fall and does not become abundant until late winter. Hence, a large release in the fall should not be seriously affected by this parasite. A second larval parasite (*Diplole* *sp.*), a tachinid, attacks the seventh instar and occurs in low concentrations throughout the year. Apparently, because in natural populations of *Anastre* the generations overlap extensively seventh instar larvae are almost always present and create a constant reservoir for this parasite. This parasite is always present but since the seventh instar populations are never large the parasite population cannot build up. By synchronizing the release eventually resulting in an extremely large population of seventh instar larvae, also synchronous, it was hoped that the parasites would fail to make a numerical response in time to significantly affect the population. An ichneumonid parasitoid (*ichneumon* sp.) is occasionally present but was not considered a threat. I expected this

viruses to break down in the second generation and abnormally high parasite populations to ultimately cause a decline in the *A. dorus* population.

The second strategy employed was that of an inundative release. Assuming that we could obtain a reasonable survival rate in the first generation a sufficient number of larvae had to be released to severely damage the plant population before parasite satiation caused a decline in the *A. dorus* population. The minimum insect concentration to achieve this was determined to be 0.2 larvae per plant based on field observation of natural populations of *A. dorus* as well as greenhouse studies using various insect concentrations.

### Methods and Materials

Eggs of *Armadia jamae* Walker were collected from *Passiflora cordata* at Palm Bay, Palm Bay Co., Florida. These were surface sterilized in a 0.02 hypochlorite solution for 30 minutes, placed in a 10% sodium thio-sulfate solution for 5 minutes (to neutralize the hypochlorite), rinsed in distilled water and attached to filter paper with a 10% cyanide glue solution. The glue was permitted to dry and the filter paper with the eggs was placed in the lid of a large food jar. Waterhyacinth leaves from plants grown in a quarantine greenhouse were similarly washed in the hypochlorite solution and placed in autoclaved large food jars. The lids were placed on the jars and sealed until the larvae emerged. These sterilization procedures were necessary to retard the growth of acid bugs enough for the larvae to eclose. Fresh leaves were added as needed for food.

The larvae obtained were kept in jars for 2-3 days. They were then placed on tables filled with waterhyacinth in a greenhouse on 25 June 1949. On 25 July half of the plants were harvested and the larvae and pupae obtained. The remainder of the plants were harvested on 2 August. Larvae obtained were placed individually in 55 dram snap top plastic pill vials and provided with fresh waterhyacinth petioles. After pupation, pupae were placed in Veribloc<sup>®</sup> in a plastic jar with a wire paper lined cage over them. Adults were permitted to emerge in the cage and a 5% sucrose solution was provided for food. They mated and the female oviposited on the newspaper lining. Eggs were collected from the wire paper and treated in the same manner as the plants collected eggs.

From 14 females I obtained 1892 eggs. Approximately 365 or 20% eclosed. Due to the failure to release these immediately high mortality



occurred in the jars and approximately only 1500 larvae survived. These were released 16 August on a small pond approximately 1.2 km south of Apopka Florida on I-75, Alachua Co., Florida. The pond had a surface area of approximately 50 sq. m. and was covered with water-hyacinths which were approximately a meter tall. From previous data I estimated the density of the plants at this site and then of year to be about 88 per sq. m. Our infestation level then was approximately 1.26 larvae per plant or 26 larvae per square meter.

A second pond 0.5 km South of the first pond was selected as a control. This site was somewhat similar than the first but the water-hyacinths were very similar in both density and height. Both ponds were fenced at intervals under the Interstate Highway and both were fenced from the same entrance.

Since I hypothesized that the effects of the insect feeding activity would be most evident after the first frost no sampling was done until 12 November. Because of the destructive nature of the sampling and the small size of the ponds and the amount of time required to process each sample the number of samples taken were necessarily small. Only three samples (0-30 sq. m.) were selected at each site and were along an east-west transect, the first being near the west bank, the second in the center, and the third near the east bank.

The larvae present at this time represented the  $P_1$  generation of those released. The height of each plant was measured as well as the plant density, leaf density, and the number of larvae per plant. Insect damage on each plant was measured in terms of both leaf and rhizome damage. The larvae were counted, the water noted and any parasitoid present were recorded. One sample (0-30 sq. m.) near the center of

of each site was collected to estimate biomass. RTI (litter) and dead material from this sample was placed in a plastic bag and returned to our laboratory. The plants were divided into perennials (leaf litter), leaves (pseudo-bulbs), rhizomes, roots, stolons, and detritus (dead plant material). They were placed in ice cream cartons and dried to a constant weight in an oven at 100° C for 2-3 da. After drying, the containers were allowed to cool to room temperature and then weighed on a Mettler 101/analytical balance.

### Result

Extensive damage by *A. dorsalis* was evident within two weeks of the release site. While the initial releases were made in one small area, the larvae rapidly spread over the entire plot. Within 50 days clustered egg masses were noted indicating the beginning of a second generation.

At the time of sampling (December 12) the crane population had increased to 32 larvae per sq. m. (Table 11) as compared to 3 per sq. m. (11/14), larvae at the control site. Most of these were 4th or 5th instar and represented the final stages of the second generation. This population was equivalent to a 50 larvae/plant at the experimental site and only a 60 larvae/plant at the control site.

One of the insects in the unusually high population at the release site were parasitized. Nearly 45% of the larvae in the relatively low population at the control site were dead as a result of parasitism.

After 10 weeks of locust feeding the plants in the release site were severely damaged. As expected, the occurrence of a 71°F frost the first week in December accentuated this damage. Many of the plants, although severely damaged by the locusts, appeared green and healthy prior to this time. The freezing temperatures killed a large percentage of these damaged leaves. At the control site only the tips of the leaves suffered damage from this initial frost. Figures 41(a)-41(d) show the release and the control sites in a sequence up to one year after the initial release. Figure 42(a) shows the release site after the first frost.



Figure 41. A photographic comparison of the waterhyacinth stands at experimental and control sites at different times of the year following the release of *Anas anas* at the latter.

- a) Experimental site shortly after the release of *Anas anas* (August 1974)
- b) Release site in October.
- c) Release site after two generations of insect damage and after the first winter freeze (January). The predominant plant is *Sagittaria*. A patch of dead waterhyacinth is noticeable to the right.
- d) The release site in the spring (March 1975). Most of the water is covered with *Sagittaria*.
- e) The release site in July 1975 as the *Sagittaria* stand begins to open up.
- f) The release site one year after the initial release (August 1975). The site is dominated by cattail (*Cyperus* sp.) Notice the small stand of waterhyacinth in the background.
- g) The control site in the spring (March 1975). Compare this with Figure 42b.
- h) The control site one year after the termination of this study. Compare this with Figure 42f.



Figure 40(a)



Figure 40(b)

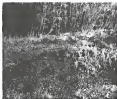


Figure 432c]



Figure 432d]



Figure 43(a)

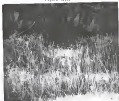


Figure 43(b)





Figure 40(a)

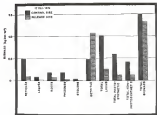


Figure 40(b)

Various characteristics of the heterozygous populations and estimates of insect damage are compared statistically in Table 11. All of the plants sampled at the control site were alive while 26% were dead at the release site. Only 17% of the control plants had damage to the rhizome while 72% of the plants had rhizome damage at the release site. Further, only 4% of the control leaves were damaged as compared to 26% at the release site. Plant density and leaf density were not significantly different between the two sites but both height and leaves per plant did decrease significantly (20% and 26% respectively). This indicates that the plants were smaller as a result of insect attack but not necessarily fewer in number.

Biomass estimates could not be compared statistically since only one sample per site was taken. Differences in biomass between the sites were obvious, however, and are illustrated in Figure 41. The changes in biomass were much greater than any of the morphological characteristics in Table 11. Standing crop (total living plant weight) at the release site was only 25% of that at the control site. The change in whole weight was greatest with a demonstrated loss of 66%. This indicates a lack of vegetative growth in the infested plants where whole production is necessary for astat production. Petioles (leaf bases) and rhizomes decreased about 60% while roots decreased only 40%. The total photosynthetic tissue (leaves and petioles) decreased more than the non-photosynthetic tissue (roots, rhizomes and rhizomes). At the release site there were 25% and 27% respectively of their values at the control site. This difference appears to be due to the smaller change in the roots, the only part not attacked by *Anomura*.

Figure 44. A comparison of the standing crop of *Leptothorax* at the control site and the release site. Total biomass includes both living and dead plant material. The phylogenetic mass (green mass) includes perennation (leaves) and perishes. The non-phylogenetic mass includes seeds, rhizomes, and stolons collectively.



Total biomass (living and dead material) was only 1/15 less at the release site than at the control site. This appears to indicate that net primary production was not dramatically reduced as a result of insect activity. The amount of this represented as detritus (dead material) more than doubled at the release site. Hence, living plant material decreased, dead plant material increased, but the total of the two showed little change.

Insect infestation did not significantly reduce the plant density. In fact, a small increase was evident. The yield (biomass per sq. m.) however, decreased. This indicates that the weight per plant decreased more than is apparent from the total standing crop. Figure 46 illustrates the biomass per plant for the various plant parts. In all cases a greater change is noted when parameterized in this manner. The change in standing crop, then, is not the result of the insects killing a portion of the plants and leaving a portion intact. This would result in a smaller standing crop but the weight per plant change would be less than or equal to the standing crop change. Further, insect attack resulted in a percentage of smaller plants. There were probably effects produced in response to an increase in available space as leaves from neighboring plants died thus reducing the amount of shading to the rest.

Since the degree of change as a result of insect attack varied with the plant parts the plant proportions must have changed. Table 13 lists the ratios of the various plant parts at both sites. In general, the plant proportions at the release site were typical of small plants. The ratio of leaf weight to plant weight was higher at both sites. The ratio of particle weight to plant weight was less at the release site probably due to the reduction in intraspecific competitive shading

**Figure 45** The mass represented by the various plant parts for an average waterhyacinth plant at both the control and release sites

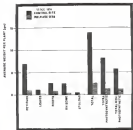


Table 33 Ratios of plant parts at the two dates on 12 December 1974

Ratios Compared	Infected Site	Control Site
Roots/plant	0.08	0.08
Stems/plant	0.48	0.58
Stems/plant	0.15	0.17
Root/plant	0.23	0.19
Stems/plant	0.62	0.63
Root + Stems/whole	1.00	0.84
Photosynthetic/plant	0.46	0.49
Non-photosynthetic/plant	0.54	0.41
Leaf/petiole	0.23	0.17
Living/dead	0.34	0.19



is less need for supporting tissue to display the leaves. The proportion of the plant represented by roots increased and the root:rhizome:shoot ratio increased. This is typical of small plants growing in open stands. The photosynthetic tissue ratio decreased relative to the non-photosynthetic tissue. This is in contrast to smaller saplings in a greenhouse (see previous section) where above:below appeared to result in a decrease in the root:rhizome:shoot ratio. Since the surviving plants had a well developed root system at the release site they would have probably recovered if the insects had been removed and if the season was favorable.

### Discussion

I assumed at the beginning of this experiment that parasite populations would increase and ultimately reduce the introduced *Aedes* densa population at the release site. By the end of the second generation, however, this had not become apparent. The population of  $F_1$  seventh instar larvae was 75% greater than the population of first instar larvae initially released. Furthermore, some of the larvae collected at the release site were used as a result of parasitism while 40% of those at the control site were. Not only did the initial population survive and reproduce contrary to my expectations but it increased in the subsequent generation which was apparently also surviving well.

Since this study was not designed to evaluate the population dynamics of *A. densa* I can only speculate on the reasons for the success of this population. I feel that by synchronizing the generations the consequences of parasitism were effectively reduced. The parasites at this site may have been "programmed" to low host populations and overlapping generations. By inundating the natural population which had individuals at various stages of development with the introduced population with individuals all at the same stage of development the synchronization of the age-specific parasites with the host may have been enhanced. For example, if parasites of the seventh instar larvae were released at the time of release of the first instar larvae the ability of the parasite population to increase would not change. Only those parasites that are present at the time that the introduced host population is at an appropriate age would have an increased chance of

propagulated success. Again, the parasite build-up would be closer than expected as long as the host population remains specialized. This assumes negligible recruitment to the parasite population from outside the release area. This is probably not a valid assumption but the parasite did fail to control *A. donax* before sufficient damage was done to the nonmycorrhizal population. I plan to conduct a similar study including a life table analysis of a field released population of *A. donax* in the future.

The response of the plant population to insect feeding tend to verify similar experiments using greenhouse cultures of watergerardia. Plant density increased a small amount but this was probably an opportunistic response to available space as the larger plants initially present died and light penetration increased. The degree of this response appears to be related to the quantity of light available and is probably seasonal in nature. The plants produced were much smaller than floating higher in the water and were probably more susceptible to temperature extremes.

A reduction in the leaf canopy was apparent as height, leaf density, number of leaves per plant, and the biomass of photosynthetic organs decreased. This does not necessarily indicate a reduction in net productivity since smaller plants tend to be more efficient than larger ones (Brown et al. 1974). The proportion of the plant represented as leaf blades did not change while the proportion represented as roots increased. The major change appeared to be in the petiole proportion which is primarily a structure for supporting and displaying the leaves. In this open stand this supportive structure would not be as important as in a dense stand. As a result the relative photosynthetic ability of the plant per gram of biomass was probably not affected but the relative ability to absorb nutrients probably increased. This is reflected in the increased root-rhizome to shoot ratio. In the greenhouse studies a decrease in the root-rhizome:shoot ratio was evident. This is in contrast to the increase noted here. Perhaps, in the former case, an insufficient amount of time was available for root regrowth prior to harvesting. The plants produced at the Folsom site in the field experiment were much more typical of small plants growing in

open about that were those in the greenhouse experiments.

The small difference in total biomass percent tends to substantiate the feeling that net productivity was not reduced. A number of explanations are possible for this. Productivity at this time of year may be low, hence what was measured was merely the amount initially present. This is possible since I have noted in other studies that the standing crop begins to decline in late summer. A second explanation is that the insect infestation decreases intraspecific competition thereby increasing the productivity of the remaining plants. This increased productivity may make up part of the difference caused by the insects.

Jensen (1961) pointed out that carbohydrate storage is directly correlated with winter hardiness. If the primary organ of carbohydrate storage in asteropachids is the rhizome (Farlow and Earl, 1966) then the feeding activity of insects strongly reduced the carbohydrate reserves. This is illustrated in Figure 61 where the rhizome weight per plant at the release site is only 18% of that at the control site. Harris (1970) stated, however, that an injury that lowers carbohydrate levels either directly or indirectly by retarding water production and growth is likely to be partly compensated for by an increase in photosynthetic efficiency.

Farlow and Earl (1966) found that the rhizome length remains fairly constant throughout the growing season. They attributed this to an equilibrium between rates of decay at the older portions and rates of increase at the crown. If this is true we may assume that carbohydrate reserves also remain fairly constant and at the end of the growing season are sufficient to sustain the plant through the winter and previous

sufficient energy for regrowth in the spring. By reducing these resources the effect of the insect infestation was that of decreasing the winter hardiness of the plants and preventing regrowth in the spring.

While total biomass showed little change between the two sites the turnover rate obviously was greater at the release site and accounted for the decrease in standing crop. This is verified in the increased detrital production. The rate of decomposing plant material was almost three times greater at the release site than at the control site.

Following the decline in the waterhyacinth population several changes in the species composition were noted at the release site. In August, at the time of release, the pond was covered with a pure stand of waterhyacinth (Figure 41(a)). By October a large proportion of the leaves were beginning to wilt and become brown and *Scheuchzeria* had begun to appear amongst the waterhyacinth plants (Figure 42(a)). In January only a few patches of dead waterhyacinth were evident (Figure 43(a)) and *Scheuchzeria* dominated the surface although there were some areas of open water. *Scheuchzeria* increased and by March (Figure 43(b)) it covered the entire surface of the pond. In July the surface had again begun to open and *Scheuchzeria* was less dominant. A mixture of *Scheuchzeria*, *Phragmites*, *Salvinia*, and *Juncus* was present and the small stand of *Scheuchzeria* had begun to expand (Figure 43(c)). Waterhyacinth was again present but only in a small patch on the southeast side. By mid-August *Scheuchzeria* was present only in small patches and *Scheuchzeria* was dominant. Waterhyacinth was present in a pure stand the whole year at the control site with the exception of a small fringe of *Scheuchzeria* which appeared in the spring.

I had expected waterhyacinth to recovers and dominate the pond at

the release site by early summer but, this did not occur. Apparently the other species had sufficient time to become established and prevent the spread of the waterhyacinth into the center of the pond. All of the plants mentioned earlier are rooted and may form a physical barrier to the waterhyacinth. The long term success in controlling waterhyacinth experienced at this site would probably not occur where the water was too deep for rooted weeds to gain a firm foothold and occupy the space available. In this situation the waterhyacinth would readily float to new water areas and again become dominant. Nevertheless, I feel that this study has shown not only that waterhyacinth is vulnerable to biological control and that this control can be achieved, at least temporarily, by the manipulation of populations of native insects. It has also shown the overall effectiveness of *Aedes dorsus* as a control agent. Harris (1981) has suggested that in some cases an egg predator infestation of one insect to reduce the infestation of a weed and a second one to keep it low. Perhaps indigenous insect populations, such as *Aedes dorsus*, can be used to initially reduce the weed infestation with subsequent releases of exotic insects, such as *Encyrtus* spp., to reach a more constant control and maintain a low weed infestation.

## CHAPTER IV

### NOTES ON THE TAXONOMY AND POPULATION DYNAMICS OF *ARANEUS DOLUS* WILK.

#### Introduction

*Araneus dolus* Walker (Bucconidae: Araneidae) is a large web spider whose larvae are semi-aquatic in habits. The taxonomy of its species group is poorly understood and deserves further attention (see Literature review section). It is obviously closely allied to the species generally included in the genus *Bellium* as both adult morphology and larval habits show striking similarities. The separation of these species into two genera is based largely on the structure of the frons and characteristics of the antennae. Todd (pers. com.) feels that the validity of these characters is questionable and two are probably convergent. He therefore proposes the combination *Bellium dolus* (Wlk.) as proper for this species and further suggests that it may be conspecific with *B. portoricensis* Wlk. as proposed by Smith (1953). Because the status of this group is questionable I have used the name *Araneus dolus* Wlk. throughout this dissertation—It must be pointed out that this may not be a valid name and future taxonomic studies are needed. While I agree that *Bellium* and *Araneus* are probably congeneric, I do not feel that *A. dolus* and *A. portoricensis* are conspecific. I have had the opportunity to observe both species in the immature stages and from the viewpoint of a naturalist they certainly appear to be distinct. In order to resolve the taxonomic relationships within this group larval characters, migratory behavior, host plant preferences, and other aspects of the life history and immature stages should be considered in a bio-systematic approach.

This study was not designed to investigate the life history of *Araneus dolus* as it was originally assumed that this had been adequately investigated by Foepf and Oliver (1961). In the course of my experiments



and field studies, however, I have accumulated many observations on the bioecology of this species which I feel are significant. I will present these observations at this point, but since the methods employed are diverse, I will wait a methods section and instead explain them as the results are presented.

#### eggs

The eggs of *A. domus* are laid in a mass on the upper surface of the leaves of *Scabiosa canadensis* (Pursh) Solms or *Androsace* sp. The egg mass is very similar to that described by Riley (1883a, p. 134) for *Aranea obliquata* (= *Aethia obliquata*) as "usually convex or plane-convex masses encased in hair, and a cream colored mucous secretion." Fogel and Otter (1957) described the masses as being covered with light yellow silky hairs. The egg masses I have observed have been tan or cream colored rather than yellow. Fogel and Otter (1958) further indicated that each egg mass contained 30-40 eggs. From 11 masses collected in 1953 from *scabiosa*(spp) I have found the eggs to be 15-48 with an average of 42 ( $\pm 14.82$  s.d.). Further, I have frequently found eggs laid singly or in groups of two or three often in the axils of a leaf near the plant base. These are usually not provided with a covering and may be left by a resting female as an artifact of a previous egg extrusion. I have frequently noted a few eggs clinging to the surfaces of curled leaves after oviposition. These remnants may account for the single oviposition noted in the field.

From these new curled leaves I have observed that the eggs are not deposited in clusters when provided with an artificial substrate (1-cm wax paper, paper). When leaf bouquets are available the eggs deposited on the leaves are usually in the typical masses. This suggests that this

clustering mode of deposition is somehow stimulated by the plant.

First instars were rarely encountered in the field. This appears to be due to their short duration, small size, and inconspicuous feeding damage. Vogel and Oliver (1968, p. 150) indicated that "young larvae were found feeding on tender basal stems and young foliage" but made no specific reference to the first instar. Smith (1916) reported that willow sawflies (Bil.) went through two feeding periods. The first was a leaf mining period in which the early instars feed in the leaf blade of *Salix* (*Salix*) *arbuscula*. The second period was a petiole period in which the older larvae burrowed into the leaf petiole. This phenomenon was also observed by Clemens (1917) with *Aspilota oblique* (Bil.) on *Spila berkeleyi* L. I have found in the laboratory that when *Aspilota* L. larvae are provided only with *Salix* petiole leaves they will form leaf mines and feed between the upper and lower epidermis. They will also feed extensively aggregating in folds in the leaf blade. In the field I have never found the first instar in leaf mines. I have found them in shallow burrows in the petiole just under the epidermis in the region of the leaf folds. I have never frequently found them at the base of the plant usually between a leaf petiole and the leaf sheath or a wrapper leaf. This is consistent with Vogel and Oliver's (1968) observations. In a few instances where I have found egg masses on *Aspilota* there are evidence of larval mines within the leaf blade. Usually it appears that the larvae migrate from the egg mass. However, small exit holes through the leaf are frequently present under an egg mass indicating that the larvae burrow through the leaf upon eclosion. These individuals which do enter the leaves would be easily overlooked and may partially account for the relatively few first instar larvae

observed in the field.

Seeded and girdled weavers are found in a variety of places. They are most often located at the base of the plant frequently between two tightly appressed petioles or under a wrapper leaf usually feeding on new leaf growth. Occasionally they will feed burrow within a petiole or shallow grooves on the outside of a petiole. By the fourth instar they become almost exclusively internal feeders, boring the petioles and feeding on the apical tip of the rhizome. By the sixth instar they create large burrows doing considerable damage to the petioles and may bore three or four centimeters into the crown. The most extensive damage is created by the seventh instar. The tunnels may extend into three or four adjacent petioles, the full length of the rhizome, even through the stem into an adjacent plant. The damage to the rhizome may be so extensive as to cause severe rotting and fragmentation.

Pupation occurs within a petiole usually in the basal portion. A pupal chamber is hollowed out and a window is opened 2-3 cm. along the pupa to permit egress of the adult. As pupation is formed although a silken suspension apparatus may be constructed below the rhizome to create the pupa within the burrow. The pupa is oriented parallel to the long axis of the petiole with the head toward the distal end. Occasionally pupation occurs in the rhizome.

The adults seem to rest during the day within the foliage of the waterhyacinth root or in the vegetation along the shoreline. They are quite active at night and are frequently collected at light traps (Green HSS). I have found in the laboratory that females lay eggs and oviposit within a few hours after emergence when caged with males in the dark. This indicates a very brief pre-reproductive period. To confirm this I

dissected a 70-day old female pupa and found fully formed eggs. It appears then that oviposition can occur almost immediately after emergence and molting.

### Fecundity

Several pupae were collected from *Seticystodes* in July 1953. These were individually placed in baby food jars which were held in sealed square boxes with stap paper lining. Upon emergence a single male was paired with a single female in a one section ice cream carton. The adults and pupae were held in an environmental chamber at 25°C, 16:8 L:D photoperiod. In all, five pairs of adults were obtained from the field collected pupae. The cartons were checked daily for eggs. The eggs were removed and counted, held in baby food jars in the manner described in Section 2, and allowed to eclose. The pupates were removed each day and the egg developmental time noted. These results are summarized in Table 14. The average fecundity was 825 eggs/female, 13-85 were laid on the first day although oviposition generally continued for three days. Fecundity was 60-75 and the average developmental time was 6-8 ds.

Fecundity was checked again when larvae were reared for a field release (Section 3). The pupae were placed in vermiculite<sup>®</sup> and held in a cage constructed of hardware cloth and lined with wax paper. Instead of feeding pairs of adults all were kept in the cage and fed a sucrose solution. A total of 44 males and 17 females were reared (♂ ♀ ratio = 1:26.7). Three females emerged after the death of the last male and did not contribute fertile eggs. From the 14 females that did mate 2003 eggs were obtained. This represents an average of 143 eggs per female. Only 4.4% of the eggs were sterile, 17.4% were fertile but failed to eclose, and 78.2% eclosed. Both of these estimates

[10% and 10% eggs] ♀ ] are lower than that of Nagel and Oliver (1993). They reported an average of 100 eggs per female with a 10% infertility based on 10 mated females.

**Table 14** Fecundity, egg viability, and egg survival for 5 female *Argemone densa* collected as pupae in the field and reared in the laboratory

No.	Weight g	Survival on first day	Average egg viability (%)	# Eggs hatched	% Hatch
1	194	62	6-8	147	66.3
2	228	74	6-8	144	61.8
3	257	68	6-8	257	68.5
4	262	68	6-6	174	47.2
5	184	62	6-8	158	70.2
<b>Σ</b>	<b>1125</b>	<b>334</b>	<b>6-6</b>	<b>710</b>	<b>60.2</b>
<b>S.E.</b>	<b>36.6</b>	<b>12.4</b>	<b>0.7</b>	<b>44.4</b>	<b>12.4</b>

### Duration of Developmental Stages

First, second, and third instar larvae were obtained from field collections and from laboratory reared material. Larvae were placed individually in 1 cc. diet cups and provided with petiole sections from either *Blattella germanica* or *Stratiolaelaps nemorum*. The cups were kept in an environmental chamber at 21° C and 16h L:8h photoperiod. The plant material was checked daily and replaced as needed. The larval instar was also checked daily and recorded for each day. Head capsule were saved and later measured. Table 15 summarizes the developmental data from this study. Only three larvae pupated and this occurred following the seventh instar. I feel that this is the typical number of instars. Other larvae shed into eighth and ninth instars before death occurred. The presence of extra instars is typical in laboratory reared *Lepidoptera* when under stress (Happé, pers. comm.). Several factors may have been responsible in this study. The cups used to contain the larvae were small. They were translucent and not transparent. The larvae may need rhizome material at some stage in their life and they were only fed petioles. Humidity was high in the cups as condensation was frequently noted. Noise, light, humidity, space, food quantity and food quality could have become stress factors ultimately resulting in these extra molts. Developmental data was included for these individuals only through the seventh instar.

Total developmental time was estimated indirectly from the greenhouse experiment testing the effects of a *Junco* damage on water-uptake (Section 1). The approximate age of the larvae was known at the time of the release. The proportion contributed as larvae, pupae, and

Table 10. Summary of experimental data for *A. taeniorhynchus*.

Host Temperature (°C) Percentage of eggs incubated (N, n)	1. Incubation time per egg (N, n)		2. Percentage viability (N, n)		3. Average time (h) between hatching and incubation (N, n)		4. Incubation time (h) between hatching and incubation (N, n)	
	n observed N (N, n)	N (N, n) per egg (N, n)	n observed N (N, n)	N (N, n) per egg (N, n)	n observed N (N, n) per egg (N, n)	N (N, n) per egg (N, n)	n observed N (N, n) per egg (N, n)	N (N, n) per egg (N, n)
20	20	1000	20	1000	20	1000	20	1000
25	20	1000	20	1000	20	1000	20	1000
30	20	1000	20	1000	20	1000	20	1000
35	20	1000	20	1000	20	1000	20	1000
40	20	1000	20	1000	20	1000	20	1000
45	20	1000	20	1000	20	1000	20	1000
50	20	1000	20	1000	20	1000	20	1000
55	20	1000	20	1000	20	1000	20	1000
60	20	1000	20	1000	20	1000	20	1000
65	20	1000	20	1000	20	1000	20	1000
70	20	1000	20	1000	20	1000	20	1000
75	20	1000	20	1000	20	1000	20	1000
80	20	1000	20	1000	20	1000	20	1000
85	20	1000	20	1000	20	1000	20	1000
90	20	1000	20	1000	20	1000	20	1000
95	20	1000	20	1000	20	1000	20	1000
100	20	1000	20	1000	20	1000	20	1000

1. Incubation time per egg (N, n) is the time (h) between hatching and incubation (N, n) for each egg (N, n) incubated (N, n) at the same temperature (N, n).

2. Percentage viability (N, n) is the percentage of eggs (N, n) that hatched (N, n) out of the total number of eggs (N, n) incubated (N, n) at the same temperature (N, n).

3. Average time (h) between hatching and incubation (N, n) is the average time (h) between hatching and incubation (N, n) for each egg (N, n) incubated (N, n) at the same temperature (N, n).

4. Incubation time (h) between hatching and incubation (N, n) is the time (h) between hatching and incubation (N, n) for each egg (N, n) incubated (N, n) at the same temperature (N, n).

5. Incubation time (h) between hatching and incubation (N, n) is the time (h) between hatching and incubation (N, n) for each egg (N, n) incubated (N, n) at the same temperature (N, n).

6. Incubation time (h) between hatching and incubation (N, n) is the time (h) between hatching and incubation (N, n) for each egg (N, n) incubated (N, n) at the same temperature (N, n).

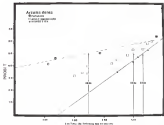
7. Incubation time (h) between hatching and incubation (N, n) is the time (h) between hatching and incubation (N, n) for each egg (N, n) incubated (N, n) at the same temperature (N, n).



and adults (estimated from pupal counts) was measured at the time of harvesting (38 and 49 days post egg collection). The larvae collected were fed particle medium until they pupated and the pupae were held until they emerged. A cumulative tally was kept on the number of adults emerging and the number of eggs deposited. These figures were later converted to daily cumulative percentages based on the final totals. The probit was derived from a conversion table for the cumulative percentage of each of these and plotted against the log of the number of days following egg collection. By fitting a line to these points the day upon which 50% of the population transformed into pupae or adults or the time at which 50% of the eggs were deposited was estimated. These probit analyses are illustrated in Figure 46. This technique should be valid since the probability of occurrence of these events is a sigmoid curve as a function of time. The vertical vectors in Figure 46 indicate the points that the probit line crosses the 5:5 probit. This represents the 50% probability for occurrence of that event and in a normally distributed population estimates the mean (see Anderson et al., 1961, p. 44). The estimated dates of oviposition, adult emergence, and deposition are 42, 50, and 52 days respectively. It may be noted that this predicts the emergence of the adults 2 days prior to pupation. This suggests a preoviposition period which is inconsistent with my previous findings. When the emergence of males and females is plotted separately, however, the predicted average emergence date for the males is 48 days and for the females 52 days. This is consistent with the lack of a prolonged preoviposition period noted earlier.

Considering that these time periods are established from the date the eggs are collected and not from the date of oviposition the

Figure 46. Probit analysis for developmental times of a grasshopper reared population of seven diets. The vertical vectors represent the times at which the 5.0 probit (50% probability) for eruption, adult emergence, and oviposition respectively were reached.

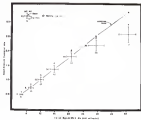


values may be underestimated. The addition of 4 da (egg developmental period) may be added to these figures to bracket the estimate. Pupa ejection occurs 40-46 da post-oviposition, adult emergence 50-56 da (males 48-54) females 52-58), and pupation 50-58 da. This conforms to the hypothetical developmental schedule given in Table 15 developed from direct laboratory observations. By summing the developmental times for each instar in Table 15 pupation is expected at 56 da post-oviposition and adult emergence at 64 da. This is considerably less than Nagel and Oliver's (1980) estimates but they reared their larvae on an artificial medium and at a lower temperature. I suspect that these two factors account for the differences.

In attempting to rear large numbers of *A. dorsalis* larvae for other experiments I have used this data to estimate the time at which I should harvest the plants to obtain primarily pupae. Eggs were collected in the field and masslar reared in the laboratory. The first instar larvae were placed on waterhyacinth plants in two large troughs in an airhouse. The plants were harvested from each trough between 41 and 46 da after the collection of the eggs. In all cases 50% or more of the insects recovered were pupae. Hence, I feel that the developmental data presented here is reasonably accurate.

The data for total capsule measurements and the larval age at each molt is summarized in Figure 47. The cross bars represent the standard deviation for each parameter and the point of intersection represents the mean. The figure to the right and the figure below represent the number of observations in the mean for the total capsule measurement and the age respectively. The figure above represents the instar these figures are derived from. I have found the total capsule

Figure 47. The head capsule diameter of *Artemia salina* larvae at each molt plotted against the larval age. The data was derived from larvae reared in water containing phenolphthalein or water lacking phenolphthalein sections, in an environmental chamber at 20°C and 14:10 L:D photoperiod. The stars represent the head capsule size of 8th and 7th instar field collected larvae and extend the trend to that expected had the larvae developed 'normally.'



measurements for the first 8 instars very useful for identifying the stages of field-collected larvae. The values for the sixth and seventh instars, however, seem to be much smaller than those from the field. These data are suspect and the smaller size may have resulted from the rearing conditions.

### Population Cycle

Vogel and Oliver (1980a) felt that disease does not limit *A. down* 2 and possibly 3 generations per year in Louisiana. Their estimate was based on their determination of the length of the development period and a 120 day winter diapause. Larvae were present at all times of the year, however, and appeared to be most abundant in September and October (Vogel and Oliver 1980a).

Larvae were sampled from 1 May 1978 to 30 April 1979 at weekly intervals on Lake Alice, Calcasieu Parish from the sampling plots described in Section 1. The larvae collected were placed in snap top pill vials and returned to the laboratory. They were maintained by feeding them waterpumpkin pickle sections. Each larva was classified as to date of the time of collection. If they died I attempted to establish the cause of death. When parasites emerged they were identified if no parasites issued shortly after the death of the larvae they were checked for disease by Dr. George Allen. Dead larvae collected in the field were handled the same way. *Pyrausta nupur* found in *A. down* larvae were collected and reared. Pupae exuviae were noted as well as the probable instar of the dead host larva.

Figure 4b illustrates the total population density of *A. down* larvae and pupae on Lake Alice for the 1978-79 sampling period. This includes all larvae both living and dead. The same data is presented in Figure 4a by individual instar. While eggs were seldom encountered by sampling they were noted in the field from September through March. This information indicates the existence of continuously breeding, overlapping generations. Eggs were most abundant in January and February which leads me to believe that no winter reproduction diapause occurs.



Figure 46

The total number of *Aranea* (sensu *Araneae*) collected, either living or dead, from the natural side of Lake Erie. Each point represents a mean per county value derived from 0.25 of samples collected in weekly intervals, from May 1924 through April 1925.



Fig. 1. Map of the study area in the northern Adriatic. Bathymetry is indicated by depth contours (0–10000 m). Sampling stations are marked with numbers 1–10.

Figure 49. The age structure of the Aramae chana population during the period of this study

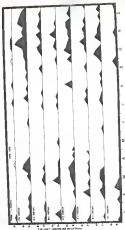


Fig. 1. Time series of monthly precipitation.

A summer decline in the population is evident from the data. From early May through late July *A. clausi* is rare on Lake Wrege. I have frequently inspected eggs during the summer for various reasons. Since they were unavailable on waterhyacinths, stands of *Amorpha* sp. at Patton Hall, Patton Co., Fla. and at Royal Pointe, Alachua Co., Fla. were checked. Eggs and larvae were found to be present throughout the summer. The population studies were conducted on this host plant but the need for these studies is evident. *Amorpha* seems to be the primary host for *A. clausi* and an understanding of the population cycles on this host would be an invaluable in interpreting seasonal population differences on waterhyacinths.

#### Mortality

Because of the lack of data with regard to egg counts I have very little information on egg mortality from populations on waterhyacinths. From 8 egg masses collected between September and December 1974 the range of egg parasitism by the wasp-like ichneumonid was seen. Mortality was between 0 and 44% (average = 38%). Because mortality was not always complete these figures are affected by the age of the eggs. Further, many egg masses were collected after the larvae and the adult parasitism had emerged and it was difficult to determine whether the chorion of a particular egg had been visited by a larva or a parasite.

To further estimate egg mortality 38 eggs were collected from a cypress thicket. The eggs were laid on pieces and were deposited in single layers rather than in the typical canvas masses. The mass was cut up so as to partition the eggs into 4 groups of 28 eggs each. These were placed on waterhyacinth leaves on a small pond near Royal Pointe on 4 September 1975. They were left on the plants for 4 days, recollected

and placed in petri dishes until all of the egg parasites emerged. By 17 September (18 days post-oviposition) 80 adults *P. uncinus* had emerged resulting in 1000 egg parasites. This leads me to believe that the layered conformation of the typical egg mass protects the inner layers of eggs from this parasite. Subsequent preliminary examinations of parasitized egg clusters indicate that only the outside layer of eggs are parasitized. The thick coating over the eggs probably prevents the parasites from working their way down to between layers. Because of the short subequator of this parasite only the outermost layer of eggs is vulnerable to attack. Since only about one third of the eggs are so protected I would expect the maximum egg mortality due to this parasite to be about 67%. I have collected eggs for rearing purposes from various locations at all times of the year and have found *P. uncinus* continually present.

Papel and Oliver (1956a) indicated that a second egg parasite, *Atractodes* sp., was present in Louisiana. I have not found this in Florida. I have found the Ichneumonid larva, *Colletes*-like *Chalcidius* Oliver, commonly feeding on the eggs of *Proctosphaera* sp. (Papel and Oliver (1956a) also list this species. I have further found an unidentified ichneumonid larva commonly attacking the eggs on *Proctosphaera*.

Figure 41 illustrates the structure of the *A. dimer* population based on larval and pupal features. The susceptibility of a particular instar to sampling is dependent upon the length of the stadium and the prominence of the damage. The duration of the seventh larval stadium is approximately three times as long as the first larval stadium. Damage by the seventh instar larva is very conspicuous and easily detected while damage by the younger larvae is less so. I believe that this accounts for the

apparent predominance of the latter stages in the life cycle. This together with the large degree of overlap between generations makes analyses of age-specific mortality factors extremely difficult.

Figure 10 illustrates the annual curves for the density of larvae and pupae collectively and population mortality. The percent mortality is derived from the number of individuals found dead in the field relative to the total living and dead. The mortality curve shows a configuration very similar to the population curve but lags slightly behind it. This would be expected when most of the mortality is due to parasitoids: higher parasitism occurs when the population is high but mortality as a result of this parasitism does not occur until somewhat later.

The data for the total annual population counts and the proportion of each instar found dead is summarized in Table 10. It is apparent that most of the mortality observed in the field occurred during the fourth and seventh larval stages. This was primarily the result of parasitism by *Comptosia* sp. (*exclusa* gr.) (*Ichneumonidae*) to the fourth instar and by *Apanteles* sp. (*Ichneumonidae*) to the seventh instar.

Figure 11 summarizes the population data for the 4th and 7th instar larvae. Illustrated for each instar is the percentage of the total found dead in the field and the percentage parasitized but still living. The dashed lines indicating the number escaping is an artifact of the number of living larvae free of parasites and pathogens. Parasitism by *Apanteles* and *Comptosia* is high throughout the year. A few 7th instar larvae die as a result of infection by the microsporidian *Beauveria bassiana* and other causes but the majority of the total observed mortality is a result of parasitoids.

Figure 50. The production of living larvae from larvae (per square meter) present in late fifth and the number of dead larvae identified as a percentage of the total



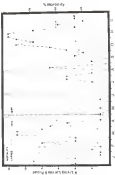
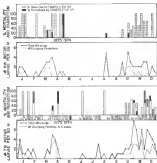


Table 16. Annual summary of larval counts and mortality.

Treatment	Total Collected	# Dead	% Mortality
1	0	0	0
2	44	1	2.27
3	37	2	5.41
4	88	29	32.95
5	28	2	7.14
6	25	2	8.00
7	43	30	69.76
Replicate	0	0	0
Rep. 6a	2	---	---
Total	274	66	23.90

Figure 5b. The total number of 4th and 7th instar dragonflies per square meter as estimated from samples taken from the wings into of Lake Alice. The solid lines represent the total number of larvae encountered. The dotted lines represent the number of that total which showed no signs of parasites or diseases. The vertical bars depict the percentage of the total affected by the various mortality factors.



Because of the extreme degree of overlap in generations and to reduce the influence of outside populations, that a natural host plant is not, any analysis of the population dynamics and mortality factors is extremely difficult. In general, I hypothesize that mortality of the eggs, 4th instar larvae, and 1st instar larvae are the important factors regulating the population. Following is a hypothetical explanation of the seasonal trends based on the available data.

During the summer, populations of host larvae are very low, hence, the parasitoid populations would be expected to be low. As a result a larval buildup becomes possible in the fall and early winter as the parasite populations fail to respond quickly enough to diminish the host. The parasite buildup is probably slow as the host population never becomes exceedingly high. As a result enough larvae escape to permit the observed fall buildup. By early winter a general decline becomes apparent in the *A. linear* population presumably as a result of the increased parasite pressure. The population appears to begin to fluctuate at this time. By late winter high mortality occurs consistently to both 4th and 1st instar larvae. The final population buildup occurs in early spring. Apparently the parasitoid population is high and allows few host larvae to escape. The few 1st instar larvae that survive to pupate emerge as adults, and develop in the spring producing progeny subject to severe parasite pressure. The majority of the larvae escaping the egg parasites are parasitized by *Chelonus* sp. and fail to survive through the fourth instar. Those that do survive are subjected to further parasitism by *Spalangia* sp. By late spring the population is at a very low level and remains so throughout the summer.

Figure 51

The number of repetitions of this factor (multiplicity of  $\lambda$  and this factor (degree index  $\lambda$ ) does not have to be subtracted from the number of points, or point number found to  $\lambda$  does have the same value of multiplicity  $\lambda$ .



Figure S2 illustrates estimates of *Aphidius rubicula* and *Coelinius* spp. populations during the study period. The parasite numbers are based on the number of pupae or puparia and the pupal exuviae found associated with dead *A. pisum* larvae. A single *Coelinius* pupa is usually found in association with a 1st instar larva although on at least one occasion two pupae were found in association with a single larva. *Aphidius*, on the other hand produces 1-6 puparia per 1st instar larva. The normal range is more on the order of 2-3. This accounts for the more prominent peaks observed in the parasite populations for *Aphidius*. Although parasite populations of both species appear to be more intense in the fall and early winter, the effects of this intensity may be tempered by the relatively high asynchronous host populations present at this time, while a large number of larvae are being removed by parasites they are replaced by younger larvae. Initially the parasites cannot respond numerically fast enough to take advantage of the newly emerged larvae.

Since the parasite populations are dependent upon the level of the host populations they remain at a fairly low level. As the parasitic populations gradually increase a subsequent decline in the larval populations begins to take place. As this continues the number of parasites present relative to the number of host larvae present increases. As a result the parasite populations are able to more fully exploit the available host populations in the spring. Ultimately the recruitment of new individuals is insufficient to replace the host population and a dramatic decline occurs. The low host populations in the summer results in a decline in the parasite populations. This permits the subsequent buildup of the larval population in the fall. It is not apparent whether the source of this fall population is the low population present earlier



or if it is the result of immigration from other populations and possibly from the other host plant (*Fraxinus*).

A parasite of *A. donea* pupa has been encountered occasionally although never from the Lake Alice population. It is an Ichneumonid (*Ichneumon confusus* Gr.) and in ten years of collecting larvae and pupae has only been found twice. I doubt that this species has a serious impact on the *A. donea* population. Vogel and Oliver (1966) listed two other species, *Ichneumon* s. sp. [Ichneumonidae] and *Microgaster confusus* (Gahan), as pupal parasites of this host in Louisiana. Table 17 is a list of the various parasites attacking *A. donea*. At least seven parasitoid taxa have been associated with *A. donea* representing 8 different families of insects. At least four of these occur in Florida.

### Discussion

*Arumia donea* Miller (1966) occurs naturally in Florida feeding on pickersweed (*Fraxinus* sp. 1) and has extended its host range to include the introduced waterhyacinth (*Eichhornia crassipes* (Mart.) Solms). The larger larvae are capable of causing serious damage in waterhyacinth when populations reach high levels. This has been observed in the field but these outbreaks are generally very localized and of short duration. Severe pressure by a diverse parasite complex appears to restrict both outbreaks and maintain *A. donea* populations at low levels in waterhyacinth.

The results of the studies from Lake Alice indicate that many of the larvae escape parasitism in the fall but since host stages are continuously available the parasite populations eventually build up and suppress the *A. donea* population. This suggests the possibility of the manipulation of *A. donea* populations for the control of waterhyacinth.

Table 2. A summary of subjects tested in parallel for *Pinus*, *A. concolor*, *Pinus nigra* (from Regel) and *Q. robur* (table 10, part 1)

Family	Species	Test, insect standard	Leaf/PC
Dieffenbachia	hololeucis variegata 50 F12	eggs	Pin., La
Euphorbia	descurainii 42	eggs	La
Euphorbia	apollinis var. var. (hololeucis)	Pin. leaflet larvae	Pin., La
Scaberrimaria	complicata 42, complex 42/43	Pin. leaflet larvae	Pin
	hololeucis 42, 43	eggs	La
	hololeucis var. hololeucis 42	eggs	Pin
Phytolacca	hololeucis var. hololeucis (hololeucis)	eggs	La

First, since the parasites are always present but in low numbers due to the relative rarity of host material perhaps large quantities of larvae may be released to replenish the natural population. If this release is made in the late summer or early fall when enough larvae are escaping parasitism to permit a natural population increase perhaps sufficient numbers of larvae may survive to cause extensive damage to the waterpockets crop before excessive mortality occurs. This is based on the assumption that the parasites will be unable to make a numerical response in time to exploit the host population.

Second, if the parasites are 'programmed' to the experimental overwintering operations of the host, possibly the host population can be forced into synchrony. The age-specific parasite population is permitted to increase as the host population increases because of the continuous availability of the proper stage host. If immediate releases are made of larvae similar in age the probability of successful parasitism by the parasite would only increase during the time period that the host population is at a suitable age. Insects the parasites issuing from previously parasitized hosts would be representative of the natural population the levels would be too low to exploit the introduced population. Further, those parasites issuing from the introduced population would not be able to further parasitize the introduced population unless its life cycle is of equal duration to that of the host. Assuming this is not the case, the majority of the parasite population would not immediately be able to locate suitable host material and the progeny of the released population would suffer low mortality.

This strategy is similar to the strategy of predator satiation

described by Lloyd and Dybas (1965) for the periodical cicada and by Jensen (1988) for ticks. In both cases it was suggested that this strategy employs a sudden increase in the population of susceptible individuals allowing them to escape before their respective predators could respond numerically. The synchronization of age involving the escape of insects from parasites may be considered part of this strategy. Thus, in effect, minimizes the time period available for successful reproduction by the age-specific parasite and again requires a rapid numerical response. Since the interval between cohorts available for a particular parasite would be maximized the probability of continued parasitism would be minimized.

Large scale testing of this theory of augmentation of the *Arum* down population is precluded by the inability to mass rear variable numbers of larvae for release. Further, a great deal of basic research on the biology and population dynamics of both *Arum* down and its parasitism should be completed. The potential for control of waterhyacinth by this insect species exists and warrants further study. It may be used in other countries simply by importing it free of parasites and predators or in this country through more complex means similar to those reported above. A thorough understanding of the host specificity of this insect, its taxonomic status, and its population mechanisms should take high priority in future studies.

### Review of Results and Suggestions for Further Studies

The productivity study discussed in the second section of this observation showed that the net solar efficiency of waterhyacinth was similar in both small and large plants [1, 21]. Removal of a large P-B cable the small plants grew faster (in terms of weight gain relative to standing crop) than the large plants.

Three phases are apparent in the annual growth of waterhyacinth on Lake Kibira. A spring growth period is characterized by an initial increase in plant and leaf density followed by an increase in plant height accompanied by a decline in plant density. This may be explained in part by energy allocation under differing conditions of density. Early in the season when the canopy is open and the plants are small, more energy is allocated towards producing offsets than towards increasing individual plant size. As space becomes more limiting more energy is put into increasing the size of the individual plant, making it more able to compete for available light, and less into offset production. In a dense stand the small offsets would probably have a small chance of surviving in the low light conditions under the canopy. It would be interesting, then, to predict that in this situation, as the plants increase further in height the small plants die which accounts for the sharp drop in absolute density.

A late summer and fall phase is defined by plant senescence and a gradual decline in plant size. This is accompanied by an equally gradual increase in plant density. An increase in canopy by *Juncus densus* will also occurred at this time but, because of multiple effects, the degree to which *J. densus* contributed to this decline is not identifiable.

Multivariate analysis failed to replicate A<sub>1</sub> down as a factor in accounting for seasonal variability in the plant characteristics. Climate was considered the most important factor regulating variables affecting standing crop. Water quality seemed to be more important in the variables associated with density. Because changes in water quality (nutrient loads) are as likely to be a result of changes in the plants as well as a cause of those changes, I am not satisfied that these models (plant and leaf density) reflect dependent relationships even though statistically "good" fits were obtained.

Intraspecific competition for light and space seems to be strongly implicated in changes in plant density. A significant negative correlation exists between plant density and plant height. Also, as the plant height distribution becomes more strongly skewed toward large plants, the number of height classes important in the total distribution drops sharply. Further, there appears to be an almost total loss of small plants during the summer when plant height is maximum.

A third phase is the winter 'no growth' or dormancy phase. During the 2-3 mo. period little change occurred in most of the characteristics observed.

Greenhouse experiments in which the levels of infestation by A. down were controlled more effectively brought out the relationship between the various plant characteristics and feeding by this insect. Repetitions of the experiment in the summer and the fall produced quite different results. In general, the plants were much more sensitive to attack by insects in the fall, and less so in the summer. Height declined in both experiments but the slope of the decline was steeper in the fall. The changes in the

number of leaves per plant were remarkably similar in both experiments. Leaf density declined in the fall but remained constant in the summer. Plant density increased with increasing insect concentration in the summer but decreased in the fall. Standing crop was only estimated in the summer but it appeared to be affected only at the highest level of infestation so that this showed in the fall an inverse linear relationship at all levels was observed.

Net community productivity did not show a dramatic decline in the fall experiment but turnover rates accelerated in direct proportion to insect concentrations. As a result, the standing crop declined even though productivity was little affected. This was not evaluated in the summer.

Also in the fall experiment a slight tendency for the proportion of the plant represented as leaves to increase under insect attack was observed as well as a tendency for the proportion represented as rhizomes to decrease. This resulted in an overall tendency for the root : rhizome: shoot ratio to decrease.

Some interesting conclusions and inferences can be drawn from the field and laboratory studies combined. These are summarized as follows:

1. Insects are apt to cause a decrease in plant size.
2. Plant density is apt to decrease with increasing plant size as a result of intraspecific competition for light and space.
3. Insects may, therefore, indirectly cause an increase in plant density by reducing intraspecific competition.
4. Both the small and large plants are equally efficient, small plants are apt to grow relatively faster by virtue of a larger P/R ratio.

5. Insects, therefore, by reducing the energy not stimulating aphid production may indirectly stimulate production.
6. This increased production may partly compensate for crop reduction by herbivory.
7. Insects reduce standing crop by exskeletoning leaves.
8. Large amounts of exskeletons are tied up as organic matter in the plants.
9. Insect feeding may, therefore, result in a faster release of these nutrients to the water which may also stimulate production.
10. Higher levels of insect herbivory are likely to be needed in the summer (probably the spring also) when solar radiation is high or saving time in the fall and winter when solar energy is low or lacking to achieve the same level of control.
11. A reduction in the size of the rhizome is proportion to the plant by insect feeding is likely to hinder the ability of the plant to survive the winter since spring responsiveness is lost from the rhizome.

During the period of these studies, natural populations of *A. downsi* were consistently low. Heavy infestation by a complex of parasites appeared to be the factor regulating population build-ups. This was very difficult to analyze, however, because of the extreme degree of overlap in generations, differential susceptibility of various tissues to sampling, and low population levels from which to derive data.

A small scale field release of *A. downsi* proved very effective in controlling a small stand of waterhyacinth. Females failed to reduce the larval population and severe damage to the plants resulted. The degree of mortality as a result of these parasites was usually less than that of a



nearby natural population. This suggests that in some situations local populations can escape persecution. The mechanism for this is not clear but it may have been due to synchronization of the age distribution in the released populations.

About one half way through this research it became apparent that *A. dunn* was almost always more abundant on pickerelweed (*Potamogeton nodosus* L.) than on waterhyacinth. These observations were casual, however, and no data has been obtained from these populations. Some important questions that should be answered soon be derived from concurrent studies of populations on both of these host plants. It would be interesting to determine if the two populations are in phase or out of phase. Is the population on waterhyacinth the result of dispersing individuals from pickerelweed after the population from the latter host builds up to a high level? Does waterhyacinth represent a secondary host allowing the population to continue while pickerelweed is scarce? Is *A. dunn* populations on both *P. nodosus* to any extent? Is there any difference in rates of paritition of *A. dunn* on the two host plants? To what extent do populations from both hosts interact? Are these two populations temporally separated? These and many other questions would greatly enhance our understanding of the observations on the *A. dunn* population reported here.

Life table studies of *Aedes* *aedes* would be helpful in evaluating methods of population regulation. Such studies of natural populations would be difficult if not impossible, however, because of the problems associated with obtaining adequate samples discussed above. A possible approach to this might be first release of subsequent life table studies of the released population.

A prerequisite to any further research on *A. dross*, however, should be a detailed bio-systematic study of the species group to which this insect belongs. Further host plant data and life history data can be accepted until the systematic relationships are established. Various countries have expressed an interest in *A. dross* for control of water-lycophids, as long as economic crops are implicated within the host range of this species. Its use in foreign countries should be discouraged. Host specificity studies with larvae from differing natural host plants should be carried out to either verify or disprove the existing host records.

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## BIOGRAPHICAL SKETCH

Ted Douglas Carter was born 15 August 1947 in Dayton, Montgomery Co., Ohio. He attended Belmont Elementary School and Belmont High School where he graduated in 1965. Following high school he attended Ohio University in Athens, Ohio for one year, after which he transferred to Foodrich College in Los Altos Hills, California. After a year in California he transferred to Northern Arizona University in 1967 from which he received his Bachelor of Science degree in Zoology in 1970 and his Master of Science degree in Biology in 1972. He transferred his studies to the University of Florida in September 1971 where he is currently completing the requirements for a Ph.D. in Entomology working on the biological control of aquatic weeds.

Ted Carter's work experience began at the age of 14 when he became employed at the Dayton Museum of Natural History. He remained on the staff working part-time during high school and full-time during the summers from 1965 through 1968. His duties included regular television appearances as a local children's show, instructing museum nature classes, presenting lectures to various civic groups, care of the museum's fine animal collection, sorting and preparing specimens for the museum's collections, and participation in various research projects. While in California he performed similar duties at the Palo Alto Children's Museum.

While in Arizona he was employed part-time in the Biology Department of A. S. U. working the insect collection and preparing bird and mammal specimens. He also worked part-time for the Zoology Department of the Museum of Northern Arizona. In the summer of 1973 he was employed by

He is a kind of the Australian division of C. I. I. O. to help collect, culture, and ship seed wasp parasites from Arizona for their biological control program. His Master's degree deals with the biology and contribution of seed beetles and their host plants.

He is a member of the Biological Society of America and the Entomological Society of America.

He is married to the former Deborah Jean Larned.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



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